PROCEEDINGS

OF THE

AMERICAN PHILOSOPHICAL SOCIETY

HELD AT PHILADELPHIA

FOR

PROMOTING USEFUL KNOWLEDGE.

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VOL. XLI. JANUARY, 1902. No. 168.

Stated Meeting, January 3, 1902.

Curator LYMAN in the Chair.

Present, 6 members.

Prof. Dana C. Munro, a newly elected member, was presented to the Chair, and took his seat in the Society.

The list of donations to the Library was laid on the table and thanks were ordered for them.

The decease of Mr. Clarence King, at Phœnix, Ariz., on December 24, 1901, aged 60 years, was announced.

Prof. A. Radcliffe Grote presented a paper entitled "Results Obtained from a Search for the Type of Noctua Linn., and Conclusions as to Types of Hubnerian Noctuid Genera Represented in the North American Fauna."

Prof. J. Dyneley Prince presented a paper entitled "A Modern Delaware Tale."

Messrs. Joseph Willcox, Joseph C. Fraley and Patterson Du Bois, the Judges of the annual election for Officers and Councillors, reported that the same had been held on this day, between the hours of 2 and 5 in the afternoon, there being present sixty duly qualified members, and that the following-named persons were elected, according to the laws, regulations and ordinances of the Society, to be the officers for the ensuing year:

President.

Isaac J. Wistar.

Vice-Presidents.

Coleman Sellers, Isaac J. Wistar, George F. Barker.

Secretaries.

I. Minis Hays, Edwin G. Conklin, Arthur W. Goodspeed, Morris Jastrow, Jr

Treasurer.

Horace Jayne.

Curators.

Charles L. Doolittle, William P. Wilson, William B. Scott.

Councillors to serve for three years.

George F. Edmunds, James T. Mitchell, Albert H. Smyth, Jcseph Wharton.

RESULTS OBTAINED FROM A SEARCH FOR THE TYPE OF NOCTUA LINN., AND CONCLUSIONS AS TO TYPES OF HUEBNERIAN NOCTUID GENERA REPRESENTED IN THE NORTH AMERICAN FAUNA.

BY A. RADCLIFFE GROTE, A.M.

(*Read January 3, 1902.*)

In view of the preparation of a general Catalogue of North American Lepidoptera, I have been asked to give the types of Hübnerian Noctuid genera. It is essential that systematists state the type of the generic title they use, and their work will be lasting in proportion as its literary basis has been proved. The scientific edifice will stand when the bricks are sound. A catalogue which employs the true, historically ascertained generic types has the advantage of possessing a permanent framework, even if later on the position of the objects designated be altered. And by using correct names a great advantage is secured to collectors and to literature. In my studies of the North American Noctuids for the

past forty years, I have had occasion to investigate the subject. The results, as to the types of our genera, are given by me in 1874, in the *Bull. Buff. Soc. N. Sciences*, and in the two following years in the *Buffalo Check List;* in 1895 in the *Abh. Naturw. Verein*, Bremen, also in the pages of the *Entomologist's Record*, London, England, Vol. vi, 27 *et seq.;* in 1900 in the *Can. Entomologist*, 209; also in publications of the *Rœmer Museum* and in these PROCEEDINGS.

In the present paper I have brought together the historical evidence as to the types of certain leading generic titles, often, perhaps commonly, used in a perverted sense, or given with a wrong authority. I have also investigated the question of the use of Noctua as a generic title in the Lepidoptera. I could not have attempted this latter without the kind aid of Mr. Jno. Hartley Durrant, of Thetford, England. The type here ascertained is *pronuba*. The name Noctua is first used by Klein in 1753 for a genus of Mollusca. Linné introduced it then, in 1758, into the Lepidoptera in his combined term Phalæna Noctua. Fabricius follows with Noctua as a generic term in 1775, 1776–77, and claims the authorship. For those who reject any limitation for the application of the law of priority, its use in 1753 will prevent its being later employed in a different group of animals. It was not used in the Birds until 1809 by Savigny, a fact to which Boisduval drew attention in 1829.

In my late List (1895) of the North American Noctuids, I gave the ascertained types; what very few corrections have been found necessary are here made. The concluding portion of this List, embracing the Catocalinæ and Hypeninæ, is not yet published. The unemployed terms in the Verzeichniss of Hübner need not be considered in the American Catalogue. They may be neglected until such time when the faunæ of Europe and America be so minutely compared, that subjective opinion can seize upon the smallest character for generic differentiation. As a rule, Hübner's genera in the Verzeichniss are of mixed contents, and I believe all having present application have been noticed by me.

In conclusion, I must thank Mr. Louis B. Prout, of London, England, and Mr. J. D. Alfken, of Bremen, for bibliographical assistance.

NOCTUA.

LINNÉ, *Syst. Naturæ*, ed. x, Holmiæ (Salvii), 1758, Phalæna Noctua.

The "Phalænæ" (496 footnote) are divided into seven groups, of which the "Noctuæ"—antennis setaceis, nec pectinatis—form the second. Linné gives the foot-structure of the larva of his "Phalæna Noctua" (497 footnote), so it seems reasonable, in a selection of the type, that this should be sought among the species whose larvæ he described. These are: Phalæna Noctua strix, fagi, bucephala, humuli, dominula, fuliginosa, iacobææ, quadra (this would be, however, excluded by Linné's nota bene), pacta, pronuba, gamma (not a "possible type" from Linné's remark—Durrant *i. l.*), festucæ, meticulosa, psi, chi, aceris, umbratica, exsoleta, verbasci, brassicæ, rumicis, oxyacanthæ, oleracea, pisi, atriplicis, præcox, triplasia, pyramidea, typica, delphinii, citrago.

If we date the commencement of our nomenclature from Linné's tenth edition, the type of "Phalæna Noctua" should then be one of these. GEOFFROY makes no use whatever of Phalæna Noctua or of Noctua, simply using Phalæna with unnamed subdivisions (Durrant *i. l.*). The earliest restriction of the species of Phalæna Noctua brought to my notice is: *Poda, Ins. Mus. Græc.*, 88–91, 1761. The species there cited from Linné are: Noctua iacobææ, quadra (not a "possible type," *vide ante*), dominula, pacta (Poda, 90: this is not Linné's species, but is *nupta* Linné, therefore the name has no effect), pronuba, gamma (not a "possible type"), exclamationis (excluded, since Linné did not describe the larva), ? secalis.

Of these species iacobææ is made the type of Hipocrita Hübn., 1806, dominula of Callimorpha Latr., 1810, and there would remain *pronuba* as the type of Noctua; exclamationis being congeneric with segetum, taken as type of Agrotis Hübn., 1806, and secalis being cited with a query. This latter is the same as didyma Esp., made the type of Apamea Ochs., 1816, through Duponchel, 1829. Before following the subsequent fate of pronuba, we will examine Linné's own restriction of his term Phalæna Noctua, which has given rise to the idea that the type of Noctua falls within the limits of Schrank's genus Catocala, the type of which I have shown to be fraxini, through Hübner's restriction in the Verzeichniss. This type covers our modern use of Catocala Schrank, 1802, which should in no case be disturbed.

LINNÉ, *Mus. Ludov. Ulr. Reginæ*, Holmiæ, 1764.

In this work Linné gives the following species: Phalæna Noctua strix, punctigerata, fulvia, ornatrix, heliconia, rubricollis (removed now to Bombyx, so that this species is excluded), fraxini, pellex. It is probable, from this restriction, the idea has arisen (communicated to me in letters) that fraxini was the type of Noctua, because rubricollis and fraxini are the only two of these species included by Linné in the Fauna Svecica, 1761, as Mr. Durrant writes me. Linné now, in 1764, excludes rubricollis, thus restricting the type to fraxini. But, since fraxini was not included by Poda in 1761, "this can be at once disregarded as of no effect."

CROTCH, *Cist. Ent.*, i, 61, 1872, writes:

Noctua—N. sponsa Lamark (1801). Cuvier and Latreille (1805) concur in this, but afterward Latreille (1810) selected N. pronuba as his type. With this selection the writer would be here agreed, and it remains to be seen what has been since done with *pronuba*.

TRIPHÆNA.

1816. OCHSENH., *Schm. Eur.*, iv, 69.

Interjecta, subsequa, comes (orbona), prosequa, consequa, linogrisea, pronuba, fimbria, ianthina (ianthe, domiduca).

1816. HUEBNER, *Verzeichniss*, 221.

Interjecta, subsequa, comes, consequa, pronuba.

1829. DUPONCHEL, *Hist. Nat. Lep. Noct.*, Tom. iv, Pt. 2, 71.

Gives pronuba as the type of Triphæna. Therefore Noctua Linn., in the Lepidoptera, and Triphæna Ochs. would be synonymous, having same type. Mr. Meyrick (1895) uses Triphæna to the exclusion of this type. And this opens up the question as to the validity of the genus, which the type-seeker is not called upon to answer in the first instance. If *pronuba*, as being type of Noctua, could not be taken as type of Triphæna, then Mr. Meyrick's use of the latter term may be correct. This question does not seem necessary to answer for the North American Catalogue.

I now follow the use of *Noctua* by authors subsequent to Linné.

FABRICIUS, *Systema Entomologiæ*, Flensburgi et Lipsiæ, 1775.

In this work 122 species are enumerated under Noctua, pp. 590–619.

FABRICIUS, *Genera Insectoruu. . . . Mantissa specierum*, Chilonii.

There is no date on title-page, but the Preface is dated Kiliæ, Dec. 26, 1776. This work is not given by Staudinger and Rebel, p. xviii, but is cited for viminalis with the date 1777. Fabricius quotes it, in 1781, as "Gen. Ins. Mant." It contains only six species under Noctua, but these are all new and constitute no restriction of those given previously. They are as follows:

(1) p. 282, Noctua boleti. This is Scardia boleti, a Tineid.

(2) p. 282, Noctua virescens. This appears to be the earliest description of the North American Noctuid Chloridea virescens Westw. ex Fab. and is neglected in the Washington Catalogue, 1893.

(3) p. 283, Noctua roboris. I cannot find this citation in Standinger and Rebel. Reference is made to Roesel, I, tab. 50, and the insect there depicted may be Dryobota roboris B., Cat. I, No. 1821.

(4) p. 283, Noctua monilis. This appears to be the earliest description of the North American Noctuid Hypsoropha monilis Hübn. ex Fab., with a wrong locality, "Anglia."

(5) p. 283, Noctua lanceolata. The habitat is given as Germany. I cannot find the citation in Staudinger and Rebel.

(6) p. 284, Noctua viminalis. This is Cleoceris viminalis, referred incorrectly in the Catalogue, No. 1560, to Bombycia. The type of Bombycia Hübn., 1806, is B. or.

FABRICIUS, *Species Insectorum*, Hamburgi et Kilonii, II, 1781.

In this work 150 species are enumerated under Noctua, pp. 209–241. The six of the Gen. Ins. Mant. are included.

FABRICIUS, *Mantissa Insectorum*, Hafniæ, II, 1787.

In this work 309 species are enumerated under Noctua, pp. 135–184, and those previously described appear to be all carried forward.

In his *Genera Insectorum*, 1776, Fabricius cites "Phalæna Linn. Geoff." as equivalent to his genus Noctua, of which he evidently considers himself the author. Fabricius restricts Phalæna (p. 164, *l. c.*) to the Geometrids, using the term in a generic sense and citing Linn. Geoff. as authority. Following his own precedent he should here have applied Linné's term Geometra. Linné's "Phalænæ," 1758, is evidently employed in a comprehensive sense, embracing all the seven groups: Bombyces, Noctuæ, etc. I have

made no search after the type of Noctua, Fabricius. It is evident he took the name from Linné, whether he credit it to him or not.

OCHSENHEIMER, *Schmetterlinge Europa's*, Vol. iv, 1816.

Ochsenheimer has no genus Noctua; pronuba is included by him in his genus Triphæna, with other yellow-winged Agrotids, differing in structure. On page viii, Ochsenheimer cites by its full title the Tentamen of Hübner, and says, literally: dieses Blatt kam mir erst lange nach dem Abdrucke des dritten Bandes zu Gesichte, daher konnte ich früher nichts davon aufnehmen. Already in 1876 I have shown that Hagen misquoted Ochsenheimer (*vide Buffalo Check List* and *Can. Ent.*), who in reality borrowed generic names and ideas from Hübner's Tentamen and properly gives him credit. Later writers, who are here so greatly indebted to their predecessors, could profitably take example.

Ochsenheimer's groupings of the Noctuids must be considered as expressing his idea of their affinities, because on page ix he says that he only catalogues and describes what he could compare in nature, not relying upon descriptions or figures, and that his systematic list is at the same time the catalogue of his collection. He gives no descriptions of his genera, any more than Hübner in the Tentamen.

BOISDUVAL, *Europæorum Lepidopterorum Index Methodicus*.

Dated on title-page 1829, but the Preface is dated Sept. 30, 1828. The work has priority over Duponchel's volume, March, 1829, or Curtis, May, 1829. "Noctua mihi," p. 63, contains names of some 70 species; Boisduval cites "Agrotis et Noctua Treits." and "Agrotis et Graphiphora Ochs." as synonymous. The type of Agrotis Hübn., 1806, segetum, is included. "*Triphæna* Ochs. Treitsch.," p. 68, contains 7 species, among them pronuba, designated by Duponchel as type.

After Fabricius, the responsibility for the use of Noctua mainly rests with Boisduval. I cannot find that Hübner ever used the term in a generic sense.

BOISDUVAL, *Genera et Index Methodicus*.

Dated on title-page and in Preface 1840.

"*Triphæna* Treits. Boisd." contains 8 species, among them Duponchel's type.

Opigena Boisd., 1840, monotypic for polygona.
Chersotis Boisd., 1840, with 8 species.
"*Noctua* Treits.," sagittifera and 18 other species.
Spælotis Boisd., 1840, for augur and 22 other species.
"*Agrotis* Ochs. Tr.," agricola and 36 other species, including *exclamationis*, designated by Duponchel in 1829 as the type of Noctua, but erroneously so, since this is taken by *Agrotis*, 1806, being congeneric with segetum. It is also excluded by Durrant as being unknown in the larval stage to Linné.

SPEYER, in the second edition of Dr. Schenckel's *Schmetterlingssammler*.

Undated, Mainz, C. G. Kunze. Has a genus "Tryphæna," as used by Ochsenheimer and Boisduval, and employs Opigena for polygona. In late editions, undated, of his popular book, "Schmetterlingskunde," Speyer continues to use *Tryphæna* (Triphæna) in Hübner's sense, and includes pronuba in its second section. These authors, therefore, regarded *Triphæna* as a distinct genus from *Agrotis*. Since I have not found in the N. Am. Noctuid fauna the precise structural equivalent of *pronuba*, it may not be necessary for the American Catalogue to use either *Triphæna* or *Noctua*. Agrotis gilvipennis *Grote*, referred by me in 1890 to *Triphæna*, belongs, I believe, having no specimen at present, to *Lampra*. It remains for the systematist to decide what species, other than *pronuba*, can be taken as type of *Triphæna*. Duponchel's type, *pronuba*, can remain, if my view that Noctua is untenable obtains.

LEDERER, *Noctuiden Europa's*, Wien, 1857.

Lederer has no genus Noctua, the species here regarded as typical being referred to one of the sections of Agrotis. Lederer divides the numerous species of Agrotis primarily upon secondary sexual characters, the male genitalia. Already, in 1874, I had proposed to divide the species into two chief groups—those species which had all the tibiæ spinose and those in which the middle and hind tibiæ alone are armed (*Bull. Buf. S. N. S.*, 11). Subsequently, in the *Canadian Entomologist*, I proposed a further addition, including the genus *Carneades*. This classification of mine gives three principal divisions for the North American species:

Front smooth, fore tibiæ unarmed: *Epilectra*, *Lampra* Hübn.
Front smooth, fore tibiæ armed: *Triphæna* O., *Agrotis* Hübn.
Front tuberculate, fore tibiæ armed: *Carneades* Grote.

Lederer makes, I believe, some structural misstatements. He gives the male antennæ of linogrisea as "pyramidal zähnig." This species is the type and sole species of *Epilectra*. Its diagnosis should read: Thoracic vestiture scaly; male antennæ simply brush-like, nearly naked; fore tibiæ unarmed; front smooth. The eyes, as in all these structures, naked. Lederer further gives agathina as having the fore tibiæ armed and triangulum unarmed, whereas the reverse appears to be the case. In depuncta the thoracic vestiture seems scaly, whereas Lederer places it in a section where this is hairy. Neither *Epilectra* or *Triphæna* (Noctua L.) need apparently affect the American Catalogue. The species referred in the "Revision" to Noctua belong to *Amathes*. Lederer's neglect of Hübner and his uncritical use of several generic names has increased the confusion, which is the more to be regretted since his structural observations are usually so valuable.

To sum up: There seems no use in disturbing Duponchel's type, *pronuba*, for Triphæna, until it is settled whether the term *Noctua* Linné can be employed. I conclude that the historically indicated type of *Phalæna Noctua* Linné is *pronuba*, and that the term *Noctua* cannot be used in the Lepidoptera because preoccupied by Klein in the Mollusca in 1753. The earliest plural form I find, which could be used, outside of Noctuæ, for the family is Apatelæ Hübner, 1806, and the family type would be Apatela aceris. The name Agrotidæ, H.-S., based on Agrotes Hübn., 1806, which latter occurs on the same page, is a more appropriate title for the whole group in Lederer's sense. Lederer himself gives no scientific title to the group. In the present case, if we exclude the term Noctua, there can be no doubt that the leading genera of the group are: Apatela, Agrotis, Hadena, Cucullia, Plusia and Catocala. Three of these belong to Schrank, 1802, and three to Hübner, 1806. Hübner's names have the preference for a family title, because he employs also the plural form, with the evident intention of using them for comprehensive groups, an intention he carries out ten years later, in 1816, in the *Verzeichniss*.

Taking the opposite conclusion, that Noctua Linn. is a valid generic title, its type being *pronuba*, then the question comes up: Is *pronuba* congeneric with *Agrotis segetum?* If so, then *Agrotis* falls before *Noctua* Linn. Meigen (1832) includes 155 species under Noctua, with Hadena, Orthosia, etc., as subgenera. His subgenus *Noctua* contains baja, candelisequa, brunnea, festiva, rhombsidea,

gothica (!), C. nigrum, triangulum, flammatra, musiva, plecta, punicea. He remarks: der Rücken hat einen Schopf. In the main this seems to be the group intended by Prof. J. B. Smith as *Noctua*, but it cannot include either pronuba or segetum. Meigen places the latter correctly under the subgenus Agrotis, but classifies *pronuba* under the distinct genus "Tryphæna" section A, which he characterizes as having the third palpal joint reduced, hardly noticeable. It does not seem as though subjective opinion would ever rest content with the reference of *pronuba* as congeneric with *segetum*, and therefore the question of the genus *Noctua* need not affect the North American Catalogue.

At the present time the study of the Noctuids in America is suffering under the evil duplication of specific names and a reckless disregard of the historically indicated types of the generic titles. In this connection may I ask how Noctua comes to be applied to the group in Prof. Smith's Revision, except by a kind of restriction? For Linné's original Phalæna Noctua contains insects belonging to several distinct families and only by some sort of literary precedent has it come to designate Owlet Moths or Noctuids. The same sort of historical research, only carried out with more exactness, reveals the types I must insist upon for certain genera. And, unless it can be shown, in any special instance, that I have erred (the study has often proved intricate), it will be clearly to the advantage of science that my results be adopted in the new N. Am. Catalogue. I now give here references I have made and the types which they reveal:

MAMESTRA.

1816. OCHSENH., *Schm. Eur.*, iv, 76.

Pisi, splendens, oleracea, suasa, aliena, abjecta, chenopodii, albicolon, brassicæ, furva, persicariæ.

1816. HUEBNER, *Verz.*, 214.

Pisi, unaminis, leucophæa. Under this restriction *pisi* became type, since Hübner's two other species are not included originally.

(March) 1829. DUPONCHEL, *Hist. Nat. Lep. Noct.*, T. iv, Pt. 2, 71.

Designates brassicæ as type, but this restriction of Mamestra is no longer possible since Hübner's action in the Verzeichniss. Hübner must have taken this generic name from Ochsenheimer,

1816; hence this part of the Verzeichniss must be of later issue, probably 1822, but at any rate earlier than Duponchel.

1874. GROTE, *Bull. Buff. S. N. Sci.*, 12.

Lists the N. Am. species and takes *pisi* as type. This accords in a general way with the modern definition of Mamestra: Hadenoid forms with hairy eyes, the non-extruded ovipositor and different larval habit separating them from Hadena (type cucubali) Schrank non Lederer (= Dianthœcia Boisd.). I list the North American species of Dianthœcia, for which name Hadena Schrank must now be substituted, and give the characters in Rev. Check List, N. Am. Noct., 1890, 13 (Bremen, Homeyer & Meyer).

HADENA.

1802. SCHRANK, *Fauna Boica*, II, 2, 158.

Refers to this genus the species of his families M. and N. These species are: typica, atriplicis, pisi, oleracea, chenopodii, præcox, xanthographa, piniperda, deaurata, referred to family M, and meticulosa, lucipara, cucubali, referred to family N. One of these twelve Noctuids must then be the type of the name of Hadena. According to modern views species 1, 2, 8, 10 and 11 are monotypic, 3–5 are Mamestrians, 6–7 Agrotids. The contents are much mixed, referable to nine genera.

1816. OCHSENH., *Schm. Eur.*, iv, 70.

Excludes all the species of Schrank's family M, but includes all of N, among his 29 species of Hadena. The mixture is now more frightful than it was at first. The three original species of Hadena—meticulosa, lucipara and cucubuli—are, however, included, and one of these three must now be the type. It is noticeable, however, although species with hairy and naked eyes are indifferently cited, that all the species of Dianthœcia are included by Ochsenheimer.

1816. HUEBNER, *Verzeichniss*, 216.

This part of the *Verzeichniss* is of later date than Ochsenheimer's volume. Hübner includes under his genus Hadena only two of Schrank's original species, typica and cucubali. The first is excluded by Ochsenheimer's first restriction in 1816, and moreover became the type of Nænia Stephens in 1829. Cucubali becomes, therefore, the type of the genus Hadena, and is to be looked upon

as the original "Trübeule." It is unnecessary, having found the type, to follow the fortunes of Hadena further. It was used improperly by Lederer for a large genus of naked-eyed species separable from Mamestra on this character.

1895. GROTE, *Ent. Record*, vi, 78.

Designates cucubali as type of Hadena, and states that *Dianthæcia* Boisduval, will probably prove synonymous.

XYLENA.

1806. HUEBNER, *Tent.*, 1.

Lythoxylea (lithoxylea) sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 85.

Vetusta, exoleta, conformis, lapidea, rizolitha, petrificata, conspicillaris, patris, spinifera, scolopacina, rurea, hepatica, polyodon, lateritia, lithoxylea, petroriza, pulla, cassinea, nubeculosa, pinastri (scabriuscula), rectilinea, ramosa, lithoriza, hyperici, perspicillaris, platyptera, antyrrhini, linariæ, opalina, delphinii. Ochsenheimer quotes Hübner and spells the genus as he does, Xylena. This is the worst of Ochsenheimer's mixtures and, while enlarging Hübner's genus, the beginning of all subsequent confusion in applying this generic title. This abuse is still being perpetuated, although I gave again the type in 1876. Later writers than Ochsenheimer take out the Lithophanoid forms (Fam. A in part, petrificata, etc.), and use for them a genus "Xylina Ochs. or Tr.," whereas Ochsenheimer has no generic term so spelled. They then reject the Hadenoid forms (Fam. B in part), which include Hübner's type lithoxylea, instead of the reverse. Hübner himself, in the *Verzeichniss*- refers lithoxylea to the same group as petrificata, and the truth seems to be that, perhaps up to Stephens, the generic types I now give to Xylena and Lithophane were thought congeneric or nearly allied. The genus Xylophasia Stephens is a synonym of Xylena Hübner, having the same type.

(1828) 1829. BOISD., *Eur. Lep. Ind. Meth.*, 86.

Cites "Xylina Tr. and Xylena Ochs.," and suppresses Ochsenheimer's reference to Hübner for the term.

(March) 1829. DUPONCHEL, *Hist. Nat. Lep.*, iv, Pt. 2, 72.

Gives vetusta as type, but this is impossible.

1876. GROTE, *Buff. Check List Noct.*, 37.

Restores Hübner's type and spelling, and gives Hadena (Lederer nec Schrank) as identical. The type of Schrank's genus was not then ascertained.

I show, in 1874, that the modern genus "Xylina" must be called Lithophane Hübn., 1816, with the type socia (petrificata)—a far more appropriate name.

The American species referred to Hadena, Lederer nec Schrank, should be catalogued under the following genera: Xylena Hübn. (=Xylophasia Steph.), type lithoxylea; Helioscota Grote, type miselioides; Oligia Hübn. (nec Grote, Smith), type strigilis; Pseudanarta Grote, type flava (crocea); Monodes Guen. (=Oligia Auct. nec Hübn.), type nucicolor (paginata). A very good notice of the species of Monodes will be found in *Entom. Am.*, Vol. v, p. 145, under the name Oligia. It may be said of all these genera, what is there said of Monodes, that they are not "strongly characterized." They have in common naked eyes, unarmed tibiæ, smooth clypeus and hadeniform cut of wing. Xylena may have a strong character in the thoracic shield of the larva. The species belonging to these genera vary from being robust, hairy and tufted down to slighter, scaly and smoother forms. To Xylena belong species like lignicolor, auranticolor, genialis, cristata, vulgaris, verbascoides, cuculliiformis, hulsti, vultuosa, sputatrix (I do not acknowledge this to be Walker's dubitans), devastatrix, occidens, arctica, violacea, Bridghami, apamiformis, lateritia, suffusea, remissa; to Helioscota: miselioides, marina, chlorostigma, mactata, modica, diversicolor. From want of space and material I do not carry these references further here.

APAMEA.

I proposed at one time to take Ochsenheimer's nictitans as type of Apamea, it is his first species; this nictitans is not the Gortyna nictitans L. of Lederer, but is nictitans Esp., a variety of secalis L.=didyma Esp.=oculea Guen. (*Cat. Staud. and Rebel*, p. 175). My reference was correct, for this species had become type of Apamea through Duponchel in 1829. The similarity of the name led me, however, to mistake Ochsenheimer's species for nictitans Bkh. (given by Lederer as of Linné)=chrysographa Hübn. (*Cat. Staud. and Rebel*, p. 186), which latter is the type of Hydrœcia Guen., as shown by me in these pages and elsewhere. It is

probable we have N. Am. species congeneric with didyma (secalis L.), but at this writing I cannot indicate them. Lederer's restriction of Apamea to testacea, which I followed in 1895, should not be accepted; this is the true type of Luperina Boisd. (see Grote, *Can. Ent.*, 1900, 211). Boisduval, in 1829, refers both nictitans (chrysographa) and nictitans (didyma) to Apamea.

PSEUDANARTA.

1878. GROTE, *Bull. U. S. Geol. Surv.*, 178.

Crocea (flava), sole species given and therefore type.

1882. GROTE, *New Check List*, New York, 27.

Flava, var. crocea, singula, flavidens, aurea. The name, without citation, is credited to Hy. Edwards, under the mistaken idea, derived from correspondence, this author had used it. *Pseudanarta* was originally proposed by Grote in letters to Hy. Edwards for this author's *Anarta crocea*.

1889. J. B. SMITH, *Ent. Am.*, v, 175.

Falcata, aurea, flava (crocea), singula, flavidens. The genus is credited to Hy. Edwards and the citation: "Proc. Cal. Ac. Sci., Vol. 6, p. 133, 1875," is supplied. But this page contains the original description of *Anarta crocea*, and the name Pseudanarta does not occur in any of the communications of Hy. Edwards to the California Academy: "Pacific Coast Lepidoptera, Nos. 1 to 22," all published. This erroneous citation is twice repeated in the Washington Catalogue, 148, 1893.

1895. GROTE, *Abh. Naturw. Ver. Bremen*, xiv, 37.

Flava, var. crocea, singula, flavidens. The genus is limited to these three species; falcata and aurea are excluded, owing to Prof. J. B. Smith's remark on their tibial structure in 1893.

COPANARTA.

1895. GROTE, *Abh. Naturw. Ver. Bremen*, xiv, 70.

Aurea, falcata, aterrima; aurea specified as type.

PLUSIA.

1806. HUEBNER, *Tent.*, 2.

Chrysitis, sole species and therefore type. This name is erroneously given to Ochsenheimer, who however cites Hübner's Tenta-

men and includes his type. Lederer in 1857 cites Plusia Fabr., but I can find no such genus in Fabricius and the name should be restored to Hübner. Chrysoptera Latr., 1825, is said to be preoc. cupied. It is used by Meigen in 1832 for concha, deaurata and moneta alone.

The names and types of the subgenera of Plusia are given by me in these PROCEEDINGS, 417 (1895). Typical N. Am. species of Plusia are: derea, dereoides, balluca, metallica (lenzi, scapularis).

GRAPHIPHORA.

1806. HUEBNER, *Tent.*, 1.

Gothica, sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 68.

Ravida and sixteen other species belonging to Agrotis in sensu Lederer, excluding Hübner's type, though taking the name from Tentamen. The confusion now commences in European literature. The genus is used for Agrotidians, with which gothica was originally held as allied, until the type is made also the type of Tæniocampa, Guenée, which must fall.

1816. HUEBNER, *Verzeichniss*, 220.

Has no genus, but a Stirps Graphiphoræ, which comprises numerous genera, mostly of Agrotidians, among them Episema, which he takes from Ochsenheimer, including gothica. No examination had been made then of the structure of the eyes and legs; pattern and size seemed at that time to warrant the juxtaposition of Tæniocampids and Agrotidians (still difficult to separate, *e. g.*, Pachnobia and Metalepsis). But the original sense of Graphiphora must be restored. Boisduval, in 1829, refers "Graphiphora Ochs." as a synonym of Noctua and Agrotis, and includes its type gothica (*l. c.*, 67) as structurally identical. This proves the accuracy of the statement given above as to the views prevalent at the beginning of the last century.

1875–76. GROTE, *Buffalo Check List*, 13, 37.

Gives the North American species, referred to Tæniocampa, to Graphiphora, and designates gothica as type. Repeats this in 1895, *Entom. Record*, 29, and last Check List, *Abh. Brem. Nat. Ver.*, xiv, and now "finally" insists.

PROC. AMER. PHILOS. SOC. XLI. 168. B. PRINTED MARCH 18, 1902.

XANTHIA.

1806. HUEBNER, *Tentamen*, 1.

Fulvago (puleacea), sole species and therefore type.

1816. OCHSENHEIMER, *Schm. Eur.*, iv, 82.

Luteago and sixteen other species. Cites Hübner, but includes his type under Cosmia. The similar endings of the names of the yellow autumnal species, in *ago*, may have helped to increase the confusion in their application which prevails in early European literature. Hübner's erroneous use of "fulvago" may have led to his generic title being misapplied. Species of Citria and Orthosia are constantly referred in America to Xanthia, which term should be kept in the North American Catalogue for paleacea alone, specimens of which I described under the name of infumata, not knowing the European species, now believed to be identical with our own. Enargia Hübn. Verz. has paleacea also for type and falls before Xanthia.

COSMIA.

1806. HUEBNER, *Tentamen*, 1.

Affinis, sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 84.

Fulvago (W. V. Hübner = paleacea), gilvago, abluta, trapezina, diffinis, affinis and pyralina. Cites Hübner's Tentamen and includes his type of Cosmia. The genus should be restored to Hübner, but has no place in our American Catalogues. Ochsenheimer corrects Hübner's erroneous application of "fulvago."

AMPHIPYRA.

1816. OCHSENH., *Schm. Eur.*, 70.

Tragopoginis, tetra, livida, cinnamomea, pyramidea, perflua, spectrum.

1829. BOISD., *Eur. Lep. Index Meth.*, 68.

Uses it for the same species. The first six species belonged since 1806 to Pyrophyla (r. Pyrophila), and the type of Amphipyra is spectrum. The genus is not represented in America. Our species belong to Pyrophyla Hübn., 1806, type pyramidea.

ACONTIA.

1816. OCHSENH., *Schm. Eur.*, iv, 91.

Malvæ, aprica, caloris, titania, solaris, luctuosa.

1816. HUEBNER, *Verzeichniss*, 257.

Malvæ, sole species and henceforth the type.

1895. GROTE, *Entom. Record*, 79.

Designates malvæ as type through Hübner's restriction. This part of Hübner's *Verzeichniss* is of later issue than Ochsenheimer's volume, from which Hübner takes such genera as *Acronicta*, *Mamestra*, *Triphæna*, etc. The genus Acontia should not be used by the American Catalogue, as it is confined to Europe. Our species belong to *Tarache*.

TARACHE.

1816. HUEBNER, *Verzeichniss*, 261.

Caloris (caffraria), solaris, insolatrix (ined.), aprica, opalina.

1874. GROTE, *Bull. B. S. N. S.*, 36.

Designates aprica as type.

ERASTRIA.

1806. HUEBNER, *Tentamen*, 2.

Amataria, sole species and therefore type. This is a genus of Geometrids and the name is erroneously applied by Ochsenheimer to a genus of Noctuids. Its use should be avoided by every careful and unprejudiced person in the Noctuids for this very good reason.

EUSTROTIA.

1816. HUEBNER, *Verzeichniss*, 253.

Unca, sole species and therefore type. The North American Noctuids referred to Erastria belong to this genus, which is used in the Catalogue of 1874, *Bull. Buff. S. N. S.*, 37, and subsequently. The change back to Erastria in the Washington Catalogue is inexcusable.

EUCLIDIA.

1806. HUEBNER, *Tentamen*, 2.

Glyphica, sole species and therefore type.

1816. OCHSENHEIMER, *Schm. Eur.*, iv, 96.

Monogramma, glyphica, triquetra, mi. Cites Hübner's *Tentamen* for name and includes his type. Ochsenheimer gives no generic description, and yet he is constantly cited as author. Hübner's property should be restored to him.

LITOGNATHA.

1873. GROTE, *Bull. Buff. Soc. N. S.*, 85.

Nubilifascia, sole species and therefore type.

1895. GROTE, *Proc. Am. Phil. Soc.*, 429.

Nubilifascia, cribrumalis. This generic name is referred in the Washington Catalogue to Hormisa Walker, but Walker's original specimen over this label we saw in 1867, and it was a specimen of Epizeuxis æmula. This determination is supported by the text of Walker's description of the genus Hormisa, which agrees with Epizeuxis and absolutely contradicts Litognatha. Litognatha should be restored.

ZANCLOGNATHA.

1857. LEDERER, *Noct. Eur.*, 211.

Tarsiplumalis, tarsicrinalis and others.

1895. GROTE, *Proc. Am. Phil. Soc.*, 424.

Tarsiplumalis, tarsipennalis and others. Tarsiplumalis may be taken as type, as stated in Buffalo Bulletin, 1874.

ROEMER MUSEUM, November, 1901.

A MODERN DELAWARE TALE.

BY J. DYNELEY PRINCE, PH.D.

(*Read January 3, 1902.*)

The chief differences between the two ancient dialects of the Lenâpe, viz., the Unami-Unalachtigo and the Minsi, have been pointed out by the late Dr. Brinton (*The Lenâpe and their Legends*, pp. 91ff.). Both these varieties of Delaware speech are still in use in a modern form—the Unami-Unalachtigo by the descendants of the Delawares who now occupy lands in Indian Territory, in the

Muskogee Agency of the Cherokee Nation, and the Minsi by about three hundred Indians in Ontario, Canada, viz., one hundred at Munceytown, one hundred at Moraviantown, the seat of a Moravian mission, and the same number at Hagersville, on the Six Nations' (Iroquois) Reserve. There are also a few Minsis at New Westfield, near Ottawa, Kansas, most of whom are under the charge of the Moravian Church.[1]

The following witchcraft story in the modern Minsi was sent to me, with other MS. material, by Mr. Nelles Montour, Chief of the Minsis at Hagersville, Ont., a well-educated Indian who writes his own language with great clearness. Like all Indian scribes, however, Chief Montour writes syllabically, separating the syllables of his texts and not the words, a process which makes a correct edition of his MSS. extremely difficult. For example, in the following tale in II. ^{b} Montour wrote *keerh keeth qta*, as three distinct syllables. This resolves itself under analysis into *keerhkee th'q'ta* 'by the fire.' His translation also is in many instances so free as rather to obscure the true meaning of the original. Thus, in IV. ^{a}, he renders *chee quack leetahhawa dulwihkawawh* 'I am a greater man than he.' The correct translation is undoubtedly 'Do not think about it; I will overcome him.' Then, too, the not always uniform, cumbrous English system of spelling followed by Montour, in common with those of his tribe who are members of the Church of England, makes an accurate analysis of his texts doubly trying. The English values of the consonants probably do not reproduce the Indian sounds with great exactness, as may be seen from Montour's constant use of the spelling *quack* 'what,' which clearly should be written *queq* (see below on III. ^{b}), as well as from his consistent omission of the *n* prefix of the first person before *g* and before the intercalary *-d-*, as in *gutauch*, I. ^{a}; *dilnoom*, III. $^{b}_{2}$, etc. The Moravian Minsis still use the much more appropriate German system of phonetics.

The analysis of the following tale has been made chiefly by means of the Old Delaware materials left by the German Moravian missionaries of the eighteenth century, tabulated in a convenient form by Dr. Brinton in his *Lenâpe-English Dictionary*.[2] In cases

[1] These details were furnished by Chief Nelles Montour, of Hagersville, Ont., and by Mr. Dew M. Wisdom, formerly Indian Agent at Muskogee, I. T.

[2] *A Lenâpe-English Dictionary*, by Daniel J. Brinton, A.M., M.D., and Rev. Albert Seqaqkind Anthony, Philadelphia, 1888. The material is drawn from a MS. dictionary preserved in the Moravian archives at Bethlehem, Pa.

where the Minsi deviates greatly from the mixed Unami-Unalachtigo dialect, in which the missionaries wrote, I have had recourse to the vocabularies of the cognate Abenaki and Ojibwe languages,[3] which have given fairly satisfactory aid in every instance save one (in V. [b]). The chief phonetic variation between Montour's dialect and the language of the Moravian missionaries is the appearance of *th* (soft, as in 'this') in Minsi as representing *s* in Unami-Unalachtigo; cp. *wsheetha* for O. D. *w'schiessa* 'his uncle,' the ending *-multhoo* for O. D. *-mallsin*, etc. Brinton asserts (*Dict.*, p. vi) that this *s* in O. D. was due to the fact that the Germans were unable to distinguish the soft *th*, which they accordingly represented by *s*. Thus Anthony, Brinton's native authority, states (*Dict.*, p. 115) that the common word for 'boy' in his language is *skahenso*, which appears in Montour's text in the form *thkuhinthoowh*, IV. [a], representing the actual pronunciation. Furthermore, in the letter from Chief Gottlieb Tobias (*Len. Legends*, p. 88) we find the form *lichsoagan* 'language,' which Montour would write *leerhthoowawgun*. In other words, those Indians who read the language according to the German system lisp the *s*.

In the following modern Minsi text these important points with regard to the pronunciation should be noted: 1. Medial and final *h* is never an aspirate, but merely a pause. 2. The combination *ng* is pronounced like *ng* in 'king.' 3. The combination *rh* is a deep guttural *gh*. Actual *r* has not existed in Lenâpe since the days of the early Swedish colony in Pennsylvania and New Jersey. It is now represented by *l* as in modern Abenaki (*l* = ancient *r*). 4. *W* before another consonant is pronounced, as in Passamaquoddy, with a short unclear vowel following it, similar to the Hebrew *Sh'va mobile*. 5. *Wh* is a guttural combination composed of *w* + *kh*. 6. The apostrophe (') indicates a very short *u*. 7. The vowels are to be pronounced exactly as in English.[4] The O. D. words are written entirely according to the German system. The Abenaki vowels are pronounced as in Italian, except the *ô*, which has the sound of the French nasal *on*. The sign ' indicates a soft guttural voice-stop similar to the Arabic medial *He*. The vowels

[3] The Abenaki material is drawn from a dictionary of the modern dialect now in course of preparation by myself, and the Ojibwe words are taken from Baraga's *Dictionary of the Otchipwe Language*, Cincinnati, 1853.

[4] Cp. Prince, "Notes on the Modern Minsi Delaware Dialect," *Amer. Journal of Philol.*, xxi, pp. 295–302.

in the Ojibwe words have the Italian and the consonants the English values.

The subject matter of Montour's tale is interesting, dealing as it does with cannibalism, a vice which was unknown among the Algonquin tribes, except in the case of wizards. In this particular story it should be noticed that the spirit *Muttontoe* (the Abenaki *Madahôdo* 'Devil') desires to devour an *aged man*. This may be a survival of the primitive time when it was actually the custom to eat the old people, apparently in order to get rid of them, as has been the case until quite recently among the Tierra del Fuego tribes. It is at least curious that the *Muttontoe* desires to eat the elderly rather than the young man, who would be a better subject for mere cannibalism. It is also very striking that the uncle becomes *sick* first and thus incapacitated. This would seem to indicate a survival of some archaic idea, concealed here under the veil of a witchcraft superstition, that the *old man* was the proper prey for the man-eater. This tale seems to embody a different principle from that shown in the Passamaquoddy account of two wizards who retired to an isolated island (Grand Manan) to devour the body of a man.[5] In the latter instance, the cannibalism was of the ordinary sacramental character, viz., the cannibals hoped to absorb some of their victim's mental qualities by devouring his flesh. It is not impossible that the custom of eating grandparents and other aged incapable persons might have had for its basis a similar sacramental idea—*i. e.*, that the old people, by entering the bodies of their descendants, should live again and at the same time impart to the younger cannibals some of the nature of the aged victims.

As literature in modern Delaware is so rare, I have given a careful philological analysis of Montour's tale, so far as my imperfect knowledge of the language has permitted.

WITHKEELNO WAUK WSHEETHA.

I. [a] Weekwaum lawee kohpe weekena withkeelno wauk wsheetha mahji kihkweelno wrhalin neepnumo. [b] Tah lickee wsheetha weenamulthoo, oonjeemawuh

A YOUTH AND HIS UNCLE.

I. [a] In a wigwam in the midst of the forest lived a youth and his uncle of many summers. [b] Once upon a time the old man was taken ill (and) called his nephew

[5] See Prince, PROC. AMER. PHILOS. SOC., xxxviii, pp. 182, 184, nr. v.

wlunquathitha aleh-mawmjeenah kihkloolaut. [c] Withkeelno lawalindum, leetahah: "gutauch wlutchawha jeeth. [d] Noolihtoomich mihtqueenootee wauk kpuheekun waukitch nooshwuhtoonich uhpeeyuhk nahtau aleenawqtheet." [e] Waupungeek andahkeshihtootah mihtqueenootee meelaun. Wsheethaha wlalindumoo wekwulup laulpuksho. [f] Nulhuh-nuh wtuhlaun wsheetha ahpeewuyuhpeenang. [g] Waupungeeka weenumultheet ithpeenurhka aleet "klithtuh." [h] Wtilawul withkeelno: "ahwanitch pawhji; cheepeenawqthoo wauk ahkonjauptoona kweeshulooqkich, shuqk chee weeshulooqkoowih; muthkuneetahaul; pawoich andah-laweetpihkahk andah-wam-quack-kaweet."

II. [a] Nulnuh peethkahkeek andah-mahji-keeshmeettheeteetah, withkeelno awuthee tindawing lmutawpoowh, pahtoon tah nij alak nih aleetpihkahk. [b] Weerhkawa quack konjwah wuhkoong; ahwan cheepeenawqthoo wcherhakahlaun keerhkee th'q'ta: [c] "Ugh," owh, "baum konjahwan nhukee; nmihwa linno. Ktuhaulaw ksheeth; naulaw; Ugh, kweeshathee." [d] Withkeelno mutahkawh weelno, shuqk wun keemoorh konjahwan weeshulooko nawkawh. [e] Nul muthkuneetaha neepahwooh; owh:—"Mawhah geesh-keeshajpinah- to say to him his last words. [e] The young man grieved (and) thought thus:—"I will make everything comfortable for my uncle. [d] I will construct a basket with (lit. and) a lid, and I will put in it all kinds of downs." [e] On the morrow, when he had finished the basket, he presented it. His uncle was pleased and received it weeping (*i. e.*, with gratitude). [f] He then placed his uncle in the soft downy bed. [g] On the morrow, the sick man stretched out his hand which meant "attention." [h] He told the youth (then):—"Some one is coming at whose terrible appearance and condition thou shalt be terrified, but fear not; take courage. He comes in the midnight hour when all things are sleeping."

II. [a] On that same night, after they had eaten, the youth sat on the opposite side of the fire, awaiting the outcome of that night. [b] Suddenly there was something overhead and a certain terrible-looking being dropped down by the fire: [c] "Ugh," said he, "I myself am here; I eat man; thou lovest thine uncle; I want him; Ugh, thou fearest me." [d] The youth had fought with wild animals (?), but this wizard, as he must be, frightened him for a while. [e] Then, summoning his courage, he stood up on his feet

wa." Owh yohquh :—" Lawpeewhich baum; keeshajpinawitch." [f] Nul ktithpihlaun aleenqahtang.

III. [a] Nul withkeelno lmutahpoowh lawpeewh wtilawul whukee yul :—[b] " Kalahaat cheepahwan. Shurhke kalahnickulooqkich jeeth. Quackwichha dilnoom? Dulmitheemich ahlihwthihkawk, tauthrha ahwanawah." [c] Withkeelno uhloomthoowh, shuqk wtilawul wsheethul:—" Lawpeewhich baum."

IV. [a] Aloorhwat quack, yih weekwaum thkuhinthoowh patchihkcheewh ; owh :—" Taunha wtindin ksheeth?" [b] (Mawshalindum) Mawsheelahwahkoo almawsheel wam wawihtoon aylackwloowheen. [c] Wauk uhloomthoowh wauk lawpeewh moorhkum weekwaum ahwawhlihkoo shawa wninahko wtil-sheewalindumoo weenawqthowh. [d] Nul wam wtilauch mookahwaun. Wtil wturhquon cheepahwan. Shawa wninootumin wuh linno nunrhat Muttuntoe. [e] Nul wtilawul withkeelno : " Chee quack leetahhawa dulwihkawah. Ktilil yoonich ktilnumin wauk ktiloohmoolin wanjich ahloowhweekahwut."

and said :—" I cannot have him ready." Again said (the wizard) :—" I shall come here once more ; let him be ready " (then). [f] Then he leapt up through the smoke-hole.

III. [a] The youth sat down again and spoke thus with himself :—[b] " Truly he is awful. It must be that my uncle shall leave me. What am I to do? I will go toward the setting sun. (Perhaps) I may find people (there)." [c] The young man (then) departed, but he said to his uncle :—" I shall come again."

IV. [a] After journeying a little, he came to a wigwam (where) a small boy came out (and) said :—" How is it with thine uncle?" [b] (The traveler) thought it strange :—" Can one so odd looking know all about our condition?" [c] And he went on, and again he found a wigwam where there was a wizard, who at once saw that he (the traveler) was in trouble ; that he looked sad. [d] Then the youth explained all to him. He described to him the terrible being. Immediately that man knew that this was Muttontoe (the evil spirit). [e] So he said to the young man :—" Do not think about it. I will overcome him. I will tell thee what thou shalt do, and I will explain to thee how to overcome him."

V. [a] Withkeelno andah-wamloohmoonda uhloomthoowh. Andah-nuhpahtah, wama wtilauch mookuhwaun wsheethul. [b] Nul andah-keeshmeetthihteet, wtulwachpeen alningich keesha-wamcheekhung neethkak. [c] Wsheethul wtuhlaun nakah wtupeenang wauk wluqknuhaun waupahthauni alpookwuhk andauch pookwuheeng, warheetawshta nakah wsheethul wtupeenang. [d] Nul wtilahmooltheen wtilkeeshich uhloowhweekwaun. [e] Nul ninandpeethkahk lawpee cheepawaun lawinda wcheerhakahlaun: "Ugh, dupih, neecheepahwaun konjawan; keeshajpe." [f] Nul andah-tahwining kpuheekun, pajkcheewh withkeelno cheepeenawqthoo uhj althithpoocheengwat uhpee. [g] Wiyoh mawhaul linnapa weeshauthoowh uhloomihlawh.

VI. [a] Withkeelno wauk wsheethul nulowhwee ayahpoowhuk.

V. [a] After the youth had been shown all, he departed. When he returned, the young man told all to his uncle. [b] Then after they had eaten, ? ? ? ? he swept up all the dirt. [c] He put his uncle in his (the youth's) bed, and covered him with a white blanket with a peep-hole in it, and he lay down on his uncle's bed. [d] Then he felt that something strengthened him (with power) to overcome. [e] In the dead hour of night, the hideous monster again dropped down in the middle (of the wigwam). "Ugh!" (he said) "I am here. I am a monster. Be ready." [f] Then when he opened the lid (of the basket bed), the young man, looking terrible, stepped out completely covered with feathers. [g] That man-eater became frightened (and) departed (through the smoke-hole).

VI. [a] The youth and his uncle are (still) living (there) contentedly.

Philological Commentary.

I. [a] *Weekwaum* (A.[6] *wigwôm*) 'house, dwelling' from √ *week*. Cp. *Weekena* 'they dwell, inhabit' (A. *w'wiginô*), of which *weekwaum* is the cognate accus.:—'they inhabit a house.' Note the use of the present tense in narration to denote past relation. *Lawee* 'in the midst of' = O. D. *lawi* and A. *nôwi* (reduplicated *nanôwiwi*) in the middle. See V.[e]. *Kohpe* 'forest' is undoubtedly

[6] A. = Abenaki; O. D. stands for Old Delaware, the mixed language of the missionaries.

AJP. = Amer. Journal of Philology.

cognate with A. *k'piwi* 'in the woods.' *Withkeelno* 'a young man,' composed of *withkee*, A. *uski*, Oj. *oshki* 'young' and *linno* 'man.' See on IV. [d]. *Wauk* 'and,' written *woak* in O. D.[1] *Wsheetha* 'his uncle' = O. D. *schiess* 'uncle'; A. *nzāsis* 'my mother-in-law's brother'; Oj. *nijishe* 'my uncle.' See I.[b], [f], but III. [c], *wsheethul* with obviative *-l*. *Mahji* 'already' = O. D. *metschi* and A. *majimiwi* 'always'; cp. Oj. *aji* 'already.' *Kihkweelno* 'old man,' from *kihkwee;* cp. O. D. *kikey* + *linno* 'man.' *Wrhalin* 'many'; cp. O. D. *chweli*. *Neepnumo* 'summer' = O.D. *nipen;* A. *niben;* Oj. *nibin*.

I. [b] *Tah lickee* = O. D. *tah likhique* 'once upon a time.' Montour had written wrongly *tan lickee* here. O. D. *likhique* 'now, about this time.' *Weenamulthoo* (O. D. *winamallsin*, A. *akuamalsi*) 'he feels sick.' *Oonjeemawuh* 'he calls him'; cp. O. D. *wuntschiman* 'he summons him,' composed of *wuntshi* 'from' and $\sqrt{ma}$ 'call'; so A. *uwikwimon* 'he calls him,' where the last part of the stem is identical with the Minsi. *Wlunquathitha* 'his nephew' = O. D. *lunk* 'nephew.' *Aleh-mawmjeenah-kihkloolaut. Aleh* 'in order that'; *mawmjeenah* = O. D. *mamtschitsch* 'for the last time' (A. *mômjessala*); *kihkloolaut* is a reduplicated participle, 3 p. anim. 'he speaks' from $\sqrt{klool}$. See Prince, AJP., xxi, p. 298, on this stem and cp. A. *kalolômuk* 'one speaks.'

I. [c] *Lawalindum*, cp. O. D. *uschuwelendam* 'he is grieved.' *Leetahah* 'he thinks' = O. D. *litchen;* A. *alidahômuk* 'one thinks.' *Gutauch* for *ngutauch* 'I will make' (it), with *n-* pref. of 1 p. and *-ch* sign of the future (A. *-ji*). *Wlutchawha* 'so that it pleases him.' The first element is *wule-* 'good,' 'pleasing' (A. *wuli*). *Jeeth* 'my uncle' for *njeeth* = O. D. *nschiess*. Montour always leaves off the *n* prefix of the first person before a consonant; cp. below III. [a]; *dilnoom dulmeetheemich*.

I. [d] *Noolihtoomich* 'I will make it'; *n* = 'I'; 1 p. prefix; *oolihtoo* 'make'; *m* is the sign of inanimate; *ich* = fut. ending. Cp. A. *nolitonji* 'I will make it.' *Mihtqueenootee* = O. D. (Zeisberger) *michtquinotees* (dim.) 'a basket, something made of sticks'; cp. A. *w'mi 'kwtonakwônô* 'they pry it open with sticks.' *Kpuheekun* = O. D. *kpahikan* 'cover, lid'; 'something to shut;' cp. O. D.

[1] A. — Abenaki; O. D. stands for Old Delaware, the mixed language of the missionaries.

AJP. — Amer. Journal of Philology.

kpahhi 'shut the door'; A. *kbaha* imv. of *kabhômuk* 'one shuts.' The subst. ending *-eekun* = A. *-higan*, as in *pask-higan* 'gun,' lit. 'a shooter' (also Passa. *-hig'n*, as in *wighig'n* 'book'). *Waukitch* = *wauk* + *itch*, fut. ending. Cp. A. *ta* 'and' + fut. ending *-ji*. *Nooshwuhtoomich* 'I will put it in,' with inan. *-m* and fut. *ich*. This stem may be cognate with Oj. *moshki* 'fill,' as in *n'moshkinadon* 'I fill it' (inan.). *Uhpeeyuhk* 'feathers'; cp. V. [f] *Ahpee* (?). *Nahtau* probably means 'down,' the soft under feathers (?). *Aleen-awqtheet* 'of all sorts' is a participle; cp. O. D. *elinaquot* 'this or that.'

I. [e] *Waupungeek* 'on the morrow' = O. D. *woapank*, Oj. *wabang* 'to-morrow'; cp. A. *wôban* 'daybreak.' See I. [g] *waupungeeka*. *Andah* is an inseparable prefix = O. D. *enda* 'when' (rel.). It is probably cogn. with Oj. *anindi* 'where?' *Keshitootah*, a partc. 3 p. 'he making it' (inan.). Cp. O. D. *gischiton* 'he makes it'; A. *ngiziton* 'I make it.' *Meelaun* 'he gives it to him'; cp. A. *w'milôn*. The ending *-ha* in *wsheethaha* seems to be a particle of asseverative force, as in *quackwich-ha*, III. [b]. *Wlalindumoo* 'he was pleased with it,' from *wule* 'good' and *-lindum*, as in *lawalindim*, I. [c]. *Wekwulup* 'he received it'; cp. A. *w'wikwnemen* 'he took it.' The stem is $\sqrt{wik}$. The ending *-up* is the sign of the imperfect; A. *-ob*; Penob. *-pan*. *Laulpuksho* 'he weeps,' from *lep*; cp. O. D. *lepakgik* 'those who weep'; *lepakawagan* 'weeping.'

I. [f] *Nulhuh-nuh* 'then'; cp. O. D. *nall* 'at last.' The first element *nul* here = the resumptive *nul*, as in II. [f], III. [a]. *Wtuhlaun* 'he puts him' is the animate form of the same stem as O. D. *hatton* inan. *Ahpeewuyuhpeenang* 'in the feather-bed'; see above on I. [d], and cp. Oj. *apishimon* 'a bed, anything to lie upon.' This word seems to contain the stems *ahpee* 'feather' and *uhpee* 'sit, lie'; cp. V. [e].

I. [g] *Waupungeeka* with temporal ending *-a* 'when,' as in A. *paiôdida* 'when they came.' See above on I. [e]. *Weenumultheet*, partc. 3 p. 'he is sick'; cp. I. [b]. *Ithpeenurhka* 'he stretches out his hand' = O. D. *schipinachgen*, from *nachk* 'hand.' The first part of the O. D. form *schipi* is cogn. with A. *siba-liljawi* 'stretch out thy hand.' *Aleet* 'that which is'; *al* = rel. particle + *eet* = participle 3 p. of verb 'to be'; cp. A. *ali-aït*. *Klithtuh* 'hearken' = O. D. *glistam*.

I. [h] *Wtilawul* 'he says to him'; *w'* pref. of 3 p. + infixed *t* before a stem beginning with a vowel + *il* 'say' + *wul* obviative

ending. Cp. A. *wdi'lôn* 'he tells him.' *Ahwanitsh* 'someone' with *itsh* fut. ending. With *ahwani*, cp. O. D. *auwen* 'who?' and 'someone'; also A. *awani;* Penob. *aweni. Pawhji* 'he will come.' Note that the fut. ending here is *-ji* as in A. Cp. O. D. *pejat*[8] 'he who comes' and A. *wbaiôji* 'he will come.' See below *pawoich* the fut. participle. *Cheepeenawqthoo* 'one who looks strange,' from *cheepeen* = O. D. *tschipin* 'strange' and *-awqthoo* 'he appears.' *Ahkonjauptoona* 'one who is' (?) from $\sqrt{konj}$ 'exist' (?). *Kweeshulooqkich* 'thou shalt fear it'; cp. O. D. *wischassin* 'he is afraid.' See below on II. [d]. *Shuqk* 'but' = O. D. *schuk. Chee weeshulooqkoowih* 'fear thou not!' *Chee* = neg. prohibitive particle, as in IV. [e]. For *weeshul* see above. The neg. ending here is *-oowih. Muthkuneetahaul* 'be brave.' The stem *muthkun* is probably cogn. with Oj. *songi-* 'brave,' as in *songideewin* 'courage.' The Minsi ending *-eetahaul* undoubtedly contains the stem seen in *leetahah* 'he thinks'; cp. I. [o], IV. [o], and see on II. [e]. *Pawoich* 'he will come'; fut. participle *pawoit* + *ch.* See above *pawhji. Andah-laweetpihkahk* 'when it was midnight' = O. D. *lawitpikat.* It is a comb. of *lawi* 'midst' and *pihkahk* 'night'; cp. A. *nôwitebakak* 'midnight.' *Andah-wam-quackkaweet. Andah* 'when'; *quack* 'thing'; also 'what?' (cp. O. D. *keco?* A. *kagui?*). It should be written *queq* and not *quack. Kaweet*, ptc. 3 p. 'it, he sleeps'; cp. A. *kawi;* Oj. *nin gawingwash* 'I fall into a deep sleep' For this whole sentence, cp. A.:—*tôni adoji mziwi kagui kawit* (in A. we usually find the recipr. form as *kawold'wak* 'they are asleep').

II. [a] *Nulnuh;* see on I. [f]. *Peethkahkeek* 'it was night'; cp. O. D. *pisgeu* 'dark'; *pisgeep* 'it was night' (*-eep* = sign of the past); cp. A. *pesgid'bakak* 'it is dark.' *Mahji* 'already'; see on I. [a]. *Keeshmeettheeteetah* 'they had eaten'; partc. 3 p. pl. *Keesh* = sign of perfect; *meetthee* 'eat' + *teet*, ending of 3 p. pl. partc.; *ah* = temporal ending as in *waupungeeka*, I. [g]. In A. *kizimitsihîdit* 'after they had eaten'; cp. O. D. *mizin* 'one eats' and *mizewagan* and *mitsuwagan* 'food' (the last form from Zeisberger). Montour renders here freely 'after the evening meal,' but this would necessitate the use of the word *ulakunipoagan* 'supper.' *Awuthee* 'opposite.' *Tindawing*, loc. 'at the fire,' from *tindey* 'fire.' *Lmutawpoowh* 'he sat'; cp. O. D. *wulumachdappin* 'he

[8] Note that *j* in O. D. has the value of consonantal *y*.

sits with his legs in front of him'—*i. e.*, on the ground. The last part of this combination contains the same root as that seen in *ahpeewuyuhpeen* (I.[f]) 'bed' and A. *abi* 'sit.' *Pahtoon* 'he waits'; cp. O. D. *pehawah, pehowen* 'he waits.' *Tah* 'how,' the same element seen in *taunha*, IV. [a]. *Nij* 'that' with fut. sign. *Alak* 'which is'; *al* = rel. particle + *ak* 3 p. ptc. ending inan. *Nih aleet* 'that which is'; cp. I. [g] and *laweetpihkahk*, I. [h].

II. [b] *Weerhkawa* 'suddenly'; cp. O. D. *wiechgawotschi* 'unexpectedly.' *Quack konjwah wuhkoong* 'something there was above.' With *wuhkoong* cp. O. D. *hokunk*, probably cogn. with A. *agudai* 'above.' *Ahwan*, see on I.[h]; *cheepeenawqthoo*, see on I. [h]. *Wcherhakahlaun* 'he jumps down' = O. D. *loaktschehellen*. *Keerhkee th'q'ta* 'by the fire.' With *keerhkee* cp. O. D. *giechgi* 'near, by' and with *th'q'ta* 'fire' cp. A. *skweda*; Passa. *skwut*; Oj. *ishkote*. This seems to be a pure Minsi expression. *Tindey* is the Unami word; see II. [a].

II. [c] *Owh* 'he said'; cp. Oj. *iwa* 'he says.' *Baum* 'here, hither'; see also II. [c]. Is this cogn. with Oj. *oma* 'here'? *Konjahwan* 'I am'; partc. 1 p. sg. See below on II. [d]. *Nhukee*, lit. 'my body' = 'I myself'; cp. III. [a], *whukee* 'himself.' In O. D. *hakey* is 'body'; cp. A. *nhaga* 'my body,' but it is not used to denote the emphatic pronoun. In Oj., however, we find *niiaw* 'myself'; lit. 'my body.' The A. pronoun *nia* 'I' may be cogn. with this. *Nmihwa* 'I eat'; cp. A. *n'môwô* 'I eat him.' In A. *mitsi* = 'eat' in general, as 'a meal,' but *môwô* means rather 'devour.' *Linno* 'man,' the same stem contained in *lenâpe* 'a male creature'; see Prince AJP., xxi, p. 298 n. 1. *Ktuhaulaw* 'thou lovest him'; *naulaw* (we expect rather *ntuhaulaw !*) 'I want him' = O. D. *ahoalan* 'love'; cp. Prince, *op. cit.*, p. 299. *Kweeshathee* 'thou fearest me.' Note ending of 1 p. *-ee*.

II. [d] *Mutahkawah* 'he fought with' = O. D. *machtagen*, perhaps cogn. with A. *miga'kamuk* 'one fights.' *Weelno* (?) 'wild animals'; so Montour, but I cannot find the stem. *Wun* demonstr. 'that'; cp. A. *wa*. *Keemoorh* 'wizard,' probably = O. D. *kemochwen* 'one who steals away something secretly.' *Konjahwan* partc. 3 p. 'as he was'; see above II. [c]. *Weeshulooko* 'he scares him.' See above on I. [h], II. [c]. *Nawkawh* = O. D. *nakewi* 'a little while'; cp. A. *n'makaiwi*.

II. [e] *Nul* is used as a resumptive exactly like Passa. *nit*, which occurs so often at the beginning of a sentence. It is a demonstra-

tive originally. Cp. *nulhuhnuh* I. [f], and *nulnuh* II. [a]. *Muthkuneetahah* 'summoning his courage.' See on I. [h]. It has the temporal ending here *-ah*, as in *waupungeeka* I. [g]. *Neepahwoowh* 'he stood erect' = O. D. *nipachton*. *Mawhah* 'not'; cp. O. D. *matta* 'not.' *Geesh* 'I can' for *ngeesh*. *Keeshajpinahwa* with neg. ending *-wa* (cp. IV. [e] and I. [h]) from *keeshajpin* 'be ready'; cp. O. D. *gischhatton* 'be ready,' also the form *keeshajpinawitch*, 3 p. imv., 'let him be ready.' A. has *kizôjo* 'he is ready.' *Yohquh* 'now again' = O. D. *yucke*, used as a sort of resumptive. *Lawpeewhich*, a comb. of *lawpee* 'again' and *peewhich* 'I shall come' (for *npeewhich*); cp. III. [a]. *Baum* 'hither'; see II. [c].

II. [f] *Ktithpihlaun* 'he jumps up'; cp. *wcherhakahlaun* 'he jumps down,' II. [b], and *uhloomihlawh* 'he goes up,' V. [f]. The ending *-ihlawh* seems to mean 'jump.' *Aleenqahtang* (loc. *-ang*) 'through the smoke-hole.' It is probably connected with O. D. *linquechin* 'look.'

III. [a] *Lmutahpoowh*, see on II. [a]. *Lawpeewh* 'again' = O. D. *lappi*. See on II. [c] *lawpeewhich*. *Wtilawul*, see on I. [h]. *Whukee*, see on II. [c]. *Yul*, pl. of *yun* (inan.); cp. A. *yûlil* 'these,' pl. of *yû* 'this' (inan.).

III. [b] *Kalahaat* 'truly' is a comb. of *kalah* = O. D. *kehella* 'verily, yes'; Penob. *kehela*, and *aat* the ptc. of 'to be.' The literal translation is 'true it is.' A. *kalaato* 'verily' is an exact equivalent of *kalahaat*. *Cheepahwan* 'one who looks horrible'; cp. O. D. *tschipilen* 'it is awful.' See V. [c]. *Shurhke* 'certainly' = O. D. *schachachki* 'surely.' *Nickulooqki-ch* 'he will leave me,' from $\sqrt{nickul}$ = O. D. *nukalan* 'forsake' + *i-*, ending of the 1 p. as in *kweeshathee*, II. [c]. For *jeeth*, see I. [c]. *Quackwich-ha; quack* with fut. ending + the particle *-ha* (see on I. [c].). The *w*-ending in *quackwich* shows that this word must really be pronounced *quackw* (so Anthony in *Len. Dict.*; *queq* under *kolku*). *Dilnoom* 'I do it' for *ndilnoom* (?). *Dulmeetheemich* 'I will go,' for *ndul-*, from *aal* (see *Len. Dict.*, under $\sqrt{aan}$ 'go'). The past of this verb is *ahloomthoowh* 'he went,' III. [c], V. [a]. *Ahlih-wthihkawk; ahlih*, rel. particle as A. *ali* 'where' + *wthihkawk* with loc. ending *-k* = O. D. *wsigau* 'sunset.' *Tauthrha* 'I (shall) find' (?). *Ahwanah* 'people,' really 'someone,' from *ahwan* (see on I. [h]).

III. [c] *Wsheethul* 'his uncle' is obviative with characteristic ending *-ul*. In I. [a], [b] and [f], Montour has written *wsheetha* (?).

IV. [a] *Aloorhwat* 'he traveling,' participle; cp. O. D. *miss-ochwen* 'he walks about.' *Quack* must mean 'somewhat.' *Yih*, dem. pron., probably 'a certain.' *Thkuhinthoowh* 'a small boy' = O. D. and Unami *skahenso* (see *Len. Dict.*, p. 115). *Patchihkcheewh* 'there came forth,' from O. D. *ktschin* 'go out'; see on V. [f]. *Taunha wtindin* = A. *tôni wdain* 'how is he?' *Ksheeth* see II. [c].

IV. [b] *Mawshalindum* and *mawsheelawahkoo* appear to be alternative synonyms. The first is written in parentheses in Montour's MS. *Almawsheel* probably means 'that (*al* = rel. particle) one so strange.' *Wam* 'all'; see I. [h]. *Wawihtoon* 'he knows it' (inan.); cp. A. *n'wawawinôwô* 'I know him.' *Aylackwloowheen* 'our condition'; *aylack* = O. D. *elek* 'as it is'; *wloowheen* 'our being thus.' I have translated it in the 3 p. for the sake of the English.

IV. [c] *Lawpeewh* 'again'; see on II. [c] and III. [a]. *Moorhkum* 'he found' = O. D. *mochgamen*. *Ahwawhlihkoo* probably 'there was a wizard' (so Montour). *Shawa* = O. D. *schawi* 'at once'; occurs also IV. [d]. *Wninahko* 'he knows'; cp. *wninootumin*, IV. [d], and Prince, *op. cit.*, p. 298. *Wtil-sheewalindumoo* 'he feels sad'; *wtil-*, pref. 3 p. (A. *wdelli-*); *sheewa* 'sad' (O. D. *schiwamallsin* 'he feels grieved'); *lindumoo*, the ending denoting a state of mind; cp. I. [c],[e]. *Weenawqthowh* 'he looks sad,' from *ween*, same stem as in *weenamulthoo*, I. [b], + *awqthowh* 'he looks,' as in *cheepeen-awqthoo*, I. [h]; II. [b].

IV. [d] *Wam*, see I. [h]; IV. [h]. *Wtilauch* seems to be a fut. 'he will tell him'; see also in V. [a]. It is probably used here vividly. *Mookuhwaun* appears to be a synonym of *withkeelno* 'youth.' *Wtilwturhquon* 'he describes to him,' from *wtil-*, pref. 3 p. + $\sqrt{wturh}$ + *quon*, ending 3 p. sing. (see Prince, *op. cit.*, p. 298). *Wninootumin*, 3 p. sing. inan. with def. *-in*, as in A. *n'wajônem awikhigan* 'I have a book,' but *n'wajônemen awikhigan* 'I have the book.' *Wuh linno* 'that man.' With *wuh*, cp. A. *wa* 'that.' *Nunrhat* is probably a participial formation as shown by *-at*. *Muttontoe* must be connected with O. D. *mattonheen* 'he curses' and *-to*, the same ending seen in *Manitto* 'Spirit.' It is clearly a cognitive of A. *madahôdo* 'evil spirit.'

IV. [e] *Chee quack leetahhawa* 'don't think anything about it,' not translated at all by Montour. Composed of *chee*, prohib. 'dont' (cp. I. [h]) + *quack* 'anything' + *leetahah* 'think' (occurs also

I. [b]). Note the neg. ending *-wa*, as in II. [a]. *Dulwihkawawh* (for *ndul-*) 'I will overcome him'; cp. *ahloowhweekahwut* 'the way to overcome him.' The stem is seen in O. D. *allowat* 'strong, mighty.' *Ktilil* 'I tell thee'; cp. A. *kdi'lel*, both from $\sqrt{il}$. *Yoonich* = *yoon* 'this' + *ich* (fut.) used here as relative 'what.' *Ktilnumin* 'thou shalt do it'; see III. [b]. *Wauk ktiloohmoolin* 'and I will explain it to thee.' The *k-* prefix = 'thee'; the ending *-ool* = 1 p. 'I' + the def. *-in*. See Prince, *op. cit.*, p. 299. *Wanjich* = O. D. *wentschi* 'for, in order that' with fut. *-ch*.

V. [a] *Andah wam loohmoonda* 'when he had shown him all' (not translated correctly by Montour); from O. D. *allohumassin* 'he shows it.' *Uhloomthoowh* 'he departed'; also III. [b], [c]; IV. [c]. Note the lack of subjects here which must be supplied by the context. I have avoided this by a passive periphrasis. With *nuhpahtah* 'return,' cp. O. D. *apatschin*.

V. [b] *Andah keeshmeetthihteet*, so in II. [a]. *Wtulwachpeen alningich* I cannot translate. Montour's MS. is confused at this point. *Keesha*, sign of perfect, as *geesh* in II. [c]; *wam* 'all'; *cheekhung*, from same stem as O. D. *tschikhammen* 'he sweeps it.' *Neethkak* 'dirt' = O. D. *niskeu*. The last part of this stem *-eethk*, O. D. *isk* seems to be cogn. with Oj. *aj-ishki* 'mud.'

V. [c] *Nakah wtupeenang* 'on his bed'; *nakah* 'on'; *wtupeenang* from *ahpee* 'bed' (cp. I. [d]) with pref. 3 p. *w'* with infixed *t* before a vowel. *Wluqknuhaun* 'he covers him'; cp. O. D. *mettachquohemen* 'he covers it' and Oj. *pada-gwanawa;* the common stem evidently being $\sqrt{kwena}$. *Waupahthauni* = O. D. *woapachsaney* 'white blanket.' *Alpookwuhk andauch pookwuheeng*, lit. 'he made a hole there in a hole'; cp. O. D. *pquihillen*. *Andauch* = *undach*. *Warheetawshta*, probably 'he lies down.'

V. [d] *Wtilamooltheen* 'he feels'; with *-mooltheen*, cp. I. [b]. *Wtilkeeshich* 'he will make him'; cp. O. D. *gisch* 'make'—*i. e.*, 'he feels someone making him (giving him power) to overcome.' *Uhlowhweekwaun;* cp. IV. [c].

V. [e] *Nin andpeethkahk*, see on II. [a]. *Lawinda* 'in the midst'; cp. I. [a]. *Dupih* 'I am (here)' from *uhpee* = O. D. *achpin* 'be in a place'; A. *abi* 'sit.' *Keeshajpe* 'be ready' (imv.), see on II. [c].

V. [f] *Andah-tahwining* 'when he opened' = O. D. *tauwunnummen* 'he opens it.' *Kpuheekun*, see on I. [d]. *Pajkcheewh* 'there

came forth'; cp. *patchihkcheewh*, IV. [a]. *Uhj* (?). *Althithpoocheengwat uhpee* 'he is covered with feathers'; see I. [d] *uhpeeyuhk*.

V. [e] *Wiyoh*, demonstr. pron. *Mawhaul linnapa* 'he who eats man'; cp. *n'mihwa* 'I devour,' II. [c]. On *linnapa* from *linno* 'man' and *-ape* 'a male' *par excellence;* the race name of the Delawares, see Prince, *op. cit.*, 295, n. l. *Weeshauthoowh*, see I. [h]; II. [c]. *Uhloomihlawh* 'he jumped up'; cp. *ktithpihlaun*, II. [f].

VI. [a] *Nulowhee* 'well, happily.' *Ayahpoowhuk* 'they dwell' from $\sqrt{ahp}$; A. *abi* 'sit.'

Stated Meeting, January 17, 1902.

President WISTAR in the Chair.

Present, 11 members.

General Wistar, in taking the Chair, returned thanks for the honor done him in election to the Presidency of the Society, and offered some remarks concerning the future welfare of the Society.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease of the following members was announced:

Cornelius Petrus Tiele, Ph.D., D.C.L., at Leyden, on January 11, 1902, aged 71 years.

Philip P. Sharples, at West Chester, Pa., on January 15, 1902, aged 91.

Prof. Alpheus Hyatt, at Cambridge, Mass., on January 15, 1902, aged 63.

The Standing Committees for the ensuing year were chosen, as follows:

Finance.—Philip C. Garrett, William V. McKean, Joel Cook.

Hall.—Joseph M. Wilson, Harold Goodwin, John Marshall.

Publication.—Henry Carey Baird, Patterson DuBois, Joseph Willcox, Amos P. Brown, William H. Furness, 3d.

Library.—George F. Barker, Albert H. Smyth, J. G. Rosengarten, Edwin G. Conklin, R. C. H. Brock.

The meeting was adjourned by the presiding officer.

Stated Meeting, February 7, 1902.

President WISTAR in the Chair.

Present, 10 members.

Hon. James T. Mitchell, on behalf of the Committee on Historical Documents, reported that arrangements had been made for the publication in full of the original journals of Lewis and Clark.

The following were elected officers to fill vacancies:

Vice-President, Prof. Samuel P. Langley.

Councilor, Prof. Ira Remson.

The Society was adjourned by the President.

Stated Meeting, February 21, 1902.

Mr. BENJAMIN SMITH LYMAN in the Chair.

Present, 3 members.

Letters were read from Prof. Samuel P. Langley, acknowledging his election to the Vice-Presidency, and from President Ira Remson acknowledging his election as a Councilor. A communication was received from the Congrès International des Orientalistes de Hanoï, announcing the opening of an International Exposition, and of a Congress of Orientalists in connection with it, at Hanoï in November next, and asking the Society's coöperation.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The meeting was adjourned by the presiding member.

Stated Meeting, March 7, 1902.

President WISTAR in the Chair.

Present, 25 members.

A letter was received from the Committee formed to arrange for the XIII International Congress of Orientalists, to be opened at Hamburg, on September 4, 1902, inviting this Society to send a special delegate to the Congress, and on motion the President was authorized to appoint a delegate to represent the Society.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease was announced at Philadelphia, on March 2, of Francis W. Lewis, M.D., aged 76 years.

The meeting was adjourned by the President.

Stated Meeting, March 21, 1902.

President WISTAR in the Chair.

Present, 9 members.

A letter was read from the Secretary of the Nobel Committees of the Royal Academy of Science at Stockholm, enclosing the Code of Statutes of the Nobel Foundation.

General Meeting, April 3, 4 and 5, 1902.

Present, 115 members.

APRIL 3.—MORNING SESSION, 10 A.M.

President WISTAR in the Chair.

The President delivered an Address of Welcome.

The Secretaries presented a communication from the Ad-

visory Committee in Astronomy of the Carnegie Institution (Prof. E. C. Pickering, Chairman), inviting suggestions regarding investigations in astronomy, which should be aided by the Carnegie Institution.

The following papers were read:

"Origin of the Oligocene and Miocene Deposits of the Great Plains," by Prof. John B. Hatcher, of Pittsburg.

"The Upper Cretaceous and Lower Tertiary Section of Central Montana," by Prof. W. B. Scott, for Mr. Earl Douglass, of Princeton.

"On South American Mammals," by Prof. William B. Scott, of Princeton.

"The Mammals of Pennsylvania and New Jersey," by Mr. Samuel N. Rhoads, of Audubon, N. J.

"The Identity of the Whalebone Whales of the Western North Atlantic," by Dr. Frederick W. True, of Washington.

Afternoon Session, 2 P.M.

President Wistar in the Chair.

The following papers were read:

"On the Molluscan Fauna of the Patagonian Formation," by Prof. W. B. Scott, for Dr. H. von Ihering, of São Paulo, Brazil.

"A Comparison between the Ancient and Recent Molluscan Fauna of New England," by Prof. Edward S. Morse, of Salem, Mass.

"Distribution of Fresh-water Decapods and its bearing upon Ancient Geography," by Prof. Arnold E. Ortmann, Ph.D., of Princeton.

"Systematic Geography," by Prof. William Morris Davis, of Cambridge, Mass.

"On Drift Casks in the Arctic Ocean," by Mr. Henry G. Bryant, of Philadelphia.

"On the Magnetic Properties of Nickel," by Mr. Joseph Wharton, of Philadelphia.

EVENING SESSION, 8 P.M.

The following papers were read:

"The Relation of the American University to Science," by President Henry S. Pritchett, of Boston.

"The Advancement of Knowledge by the Aid of the Carnegie Institution," by President Daniel C. Gilman, of Baltimore.

APRIL 4.—MORNING SESSION, 10 A.M.

Vice-President LANGLEY in the Chair.

The following papers were read:

"Results of Observations with the Zenith Telescope at the Sayre Observatory," by Prof. Charles L. Doolittle, of Philadelphia.

"On a New Method of Transiting Stars," by Prof. Monroe B. Snyder, of Philadelphia.

"On the Evolution of Martian Topography," by Mr. Percival Lowell, of Flagstaff, Ariz.

"Historical Investigation of the Supposed Changes in the Color of Sirius since the Epoch of the Greeks and Romans," by T. J. J. See, Ph.D., of Washington.

"Recent Progress in the Lunar Theory," by Prof. Ernest W. Brown, F.R.S., of Haverford, Pa.

"On the Spectra of Gases at High Temperature," by Prof. John Trowbridge, of Cambridge, Mass.

EXECUTIVE SESSION, 12.40 P.M.

President WISTAR in the Chair.

Pending nominations were read, and the candidates for membership were balloted for, and the Secretaries reported the election of the following:

Residents of the United States—

John A. Brashear, Sc.D., Allegheny, Pa.

Andrew Carnegie, LL.D., New York.
Prof. William B. Clark, Baltimore.
Prof. Hermann Collitz, Ph.D., Bryn Mawr.
Grove K. Gilbert, Washington.
President Arthur Twining Hadley, New Haven.
Prof. George E. Hale, Williams Bay, Wis.
Prof. Paul Haupt, Baltimore.
Prof. Albert Abraham Michelson, Sc.D. (Cantab), Chicago.
C. Hart Merriam, Washington.
Prof. Theodore William Richards, Cambridge, Mass.
Prof. Felix E. Schelling, Ph.D., Philadelphia.
Prof. Robert Henry Thurston, Ithaca.
Benjamin Chew Tilghman, Philadelphia.
Prof. Robert S. Woodward, New York.
Foreign Residents—
Antoine-Henri Becquerel, Paris, France.
Jean-Gaston Darboux, Paris, France.
Sir Michael Foster, F.R.S., D.C.L., Cambridge, Eng.
Prof. G. Johnstone Stoney, F.R.S., London, Eng.
Prof. Silvanus P. Thompson, F.R.S., London, Eng.

AFTERNOON SESSION, 2 P.M.

President WISTAR in the Chair.

The following papers were read:

"Is Scientific Naturalism Fatalism? A one-minute paper" by Prof. William Keith Brooks, of Baltimore.

"On Dichotoma, a New Genus of Hydroid Jelly-Fish," by Prof. William Keith Brooks, of Baltimore.

"On Some Equations Pertaining to the Propagation of Heat in an Infinite Medium," by Prof. A. Stanley Mackenzie, of Bryn Mawr, Pa.

"On the Law of Magnetic Hysteresis," by Prof. M. I. Pupin, of New York.

"On the Continuity of Protoplasm," by Prof. Henry Kraemer, of Philadelphia.

"The Embryology of a Brachiopod," by Prof. Edwin Grant Conklin, of Philadelphia.

"Relationship of the Gordiacea," by Prof. Thomas H. Montgomery, Jr., of Philadelphia.

"The Spermatogenesis of Oniscus Asellus, Linn., with Especial Reference to the History of the Chromatin," by Prof. E. G. Conklin, for M. Louise Nichols, Ph.D., of Philadelphia.

"The International Catalogue of Scientific Literature," by Cyrus Adler, Ph.D., of Washington.

APRIL 5.—MORNING SESSION, 10 A.M.

Vice-President SELLERS in the Chair.

The following papers were presented:

"Experiments on Cytolysis," by Prof. Simon Flexner, of Philadelphia.

"A Classification of Economies," by Prof. Lindley Miller Keasbey, of Bryn Mawr, Pa.

"On Osteitis Deformans," by Prof. James C. Wilson, of Philadelphia.

"The Influence of Acute Alcoholic Intoxication upon Certain Factors Involved in the Phenomena of Hæmotolysis and Bacteriolysis," by Prof. A. C. Abbott, of Philadelphia.

"Blindness from Congenital Malformation of the Skull," by Charles A. Oliver, M.D., of Philadelphia.

"The Isthmian Canals," by Prof. Lewis M. Haupt, of Philadelphia.

"Race Elements in American Civilization (illustrated by German Examples)," by Prof. M. D. Learned, of Philadelphia.

THE EMBRYOLOGY OF A BRACHIOPOD, TEREBRATULINA SEPTENTRIONALIS Couthouy.

EDWIN G. CONKLIN, PH.D.

(FROM THE ZOOLOGICAL LABORATORY OF THE UNIVERSITY OF PENNSYLVANIA.)

Plates I–X.

(*Read April 4, 1902.*)

I. INTRODUCTION.

1. *Historical.* — Although Brachiopoda are chiefly notable because of their great abundance in past geological periods, their relationships to other groups of animals are still so obscure as to make them objects of great interest to the general morphologist. At different times and by different investigators they have been variously regarded as allied to Mollusca, Polyzoa, Annelida, Chætognatha and Phoronis, while others have regarded them as a distinct phylum of the animal kingdom. Even at the present time there is no uniformly accepted view as to their relationships, all of the above affinities (excepting possibly the first) being maintained by different authors. Of the two morphological methods of investigating relationships, viz., Comparative Anatomy and Comparative Embryology, the former has been applied to this group of animals in a number of noteworthy cases. Not to mention the large number of older and less important works on this group, the comprehensive studies of Albany Hancock ('58) and the excellent researches of Lacaze-Duthiers ('61), which are still models of accuracy, the extended labors of Davidson ('86–'88) and most recently the series of splendid contributions by Blochmann ('92 and 1900) have made us as well acquainted with the anatomy of the brachiopods as we are with the anatomy of most other invertebrates.

The case stands far differently with the embryology of this group. But two writers have as yet attempted to deal with the entire embryology of a brachiopod, and both of these studies were made without the employment of serial sections or modern microscopical and micro-technical aids.

Neglecting the isolated observations of Fritz Müller ('60 and '61) of a free-swimming larval brachiopod, and the more extended but still very fragmentary observations of Lacaze-Duthiers ('61) on the development of *Thecidium*, the credit of having made the first study of the entire development of a brachiopod belongs to the

American naturalist, Prof. E. S. Morse ('71–'73). How thorough and complete this work was I shall have occasion to remark in the further course of this paper; but done as it was at a time before good microtomes and imbedding means were invented, and long before serial sections were thought of, it could not but leave much of the internal structure of the embryo undetermined, especially as the eggs and embryos of the form studied (*Terebratulina septentrionalis*) are quite small and opaque. Nevertheless Morse's work stands to-day as one of the two most important works on the embryology of the brachiopods. The other work referred to is the later but more detailed and comparative "Observations on the Development of Brachiopods," by the great Russian zoölogist, Alexander Kowalevsky (1874). Kowalevsky's work, which was published in Russian, remained practically unknown to those not acquainted with that tongue until 1883, when Oehlert and Deniker published an excellent abstract of it. In this work Kowalevsky describes his observations on the development of four species—*Argiope* (*Cistella*) *neapolitana, Thecidium mediterraneum, Terebratula minor* and *Terebratulina caput-serpentis;* only a few observations were made on the development of the two last-mentioned species, but his work on *Cistella* and *Thecidium* was detailed in character and nearly complete so far as the stages of development are concerned. Although Kowalevsky employed isolated sections to a limited extent in his work and also shows certain details of internal structure in many figures of entire embryos, yet his work of necessity left many important problems of structure unsolved.

In 1879 Prof. W. K. Brooks discovered the free-swimming larvæ of *Lingula* (*Glottidia*) *pyramidata* and described in detail the structure and further development of these larvæ up to the adult condition. This work, although dealing only with the larval stages and metamorphosis, is still the most complete extant on the development of the Ecardines, the most primitive group of the brachiopods. With characteristic insight Brooks has used his many important discoveries on the later development of *Glottidia* in an extremely valuable discussion of the systematic position of the brachiopods.

The small portion of Shipley's (1883) paper on *Argiope* (*Cistella*) which treats of the development of that form adds little to the much more extensive work of Kowalevsky on that animal. His principal contribution consists in his determination of the fact that

the so-called "segments" of the larva are not true segments, as Kowalevsky supposed, but are mere folds in the body wall.

The papers by Beecher ('91, '92, '93) on the development of brachiopods deal almost entirely with the developmental changes which occur in the shell and not with the general embryology. Beecher has proposed a very interesting and important classification of the brachiopods based on the developmental characters of the shell; since however the present work deals only with the early embryology, we need not further consider Beecher's work here.

2. *Material.*—For the material which has formed the basis of this study I desire at the outset to express my profound obligations to my friend Dr. Edward G. Gardiner, of Wood's Holl, Mass. Dr. Gardiner had collected the material (which consists of about thirty different stages in the early embryology of *Terebratulina septentrionalis*, forming a fairly complete series from the unsegmented egg up to the beginning of the metamorphosis) at Eastport, Me., during the early summer of 1894. For various reasons he was prevented from making an immediate study of this material, and when in the summer of 1898 in conversation with him I expressed my desire to study the cell lineage of a brachiopod, he graciously offered me the material which he had collected with the request that I should use it in any way I might see fit. I soon found that it would be impossible to work out the cell lineage, not only because of a lack of sufficient number of cleavage stages, but also and chiefly because of the great difficulties which the material itself offered; the eggs were quite opaque and, except in a few cases, it was impossible to render the nuclei visible in preparations of the entire egg; the cleavage was almost entirely equal and I was unable to find any constant landmarks which might be used in orientation, and finally the cleavage was found to be more or less irregular and inconstant. I was compelled therefore to abandon the plan to study the cell lineage of *Terebratulina* and the material was laid aside, until a few months ago I found opportunity to again take up this subject with the view of working out the early development of this interesting animal in as great detail as the material would allow.

3. *Methods.*—All the material was, I believe, preserved in Perenyi's fluid, and while the general form and size of the embryo as a whole, and also of its constituent cells and nuclei, has been faithfully preserved, every trace of the cilia, which according to Morse ('71–'73) cover the surface and line the alimentary tract and

body cavity, has entirely disappeared. The method of fixation, together with the long residence of the material in alcohol, rendered it difficult to stain. The picro-hæmatoxylin, which I have used with such good results in other cases, was of little value here, and I have found that in the preparation of entire eggs or embryos the most useful stain is borax carmine, while in the preparation of sections iron hæmatoxylin has given the best results. Both entire preparations and serial sections were mounted in balsam and studied and drawn under an immersion lens (Zeiss. Apochromat. 3 mm., Comp. Occ. 4).

Perhaps I may be pardoned a word in defense of the rather large use of surface views and optical sections which I have made in this paper. This has not been due to the fact that I have made few serial sections, for I have made and studied serial sections of many hundreds of embryos, but because with material which is at all favorable the orientation of the embryo and the interrelation of its various parts can be more safely and satisfactorily determined from the study of whole embryos than by means of serial sections; and this is especially true where it is possible to use an immersion lens in the study of entire preparations. Further, more points of structure can be shown in a single figure of this kind than in dozens of figures of serial sections. Of course, serial sections must always be used in connection with the study of entire preparations, and in the present paper all the details of internal structure which are shown in the surface views and optical sections have been confirmed again and again by serial sections. Any one accustomed to the study of both entire preparations and serial sections knows that few things are more deceptive than the latter when not checked by a study of the former, while the publication of whole series of sections contributes more to the pride of the author and the income of the illustrator than to the edification of the reader.

II. The Egg and its Cleavage.

Morse ('71) has described the method of egg laying, and has called attention to the fact that the mature eggs are usually kidney-shaped, though they vary considerably in shape and size. None of the unsegmented eggs which I have examined are kidney-shaped; they are slightly elliptical, being about 160 μ in the longest diameter and 144 μ in the shortest. This elongation of the egg in one

axis is probably the precursor of the first cleavage at right angles to that axis. Morse ('73) also mentions the presence of a "distinct granular membrane, the ovishell, which is formed while the eggs are still in the perivisceral cavity." I have found this membrane in all early stages (Figs. 1–10), though I have not been able to recognize it after about the twenty-cell stage. From the fact that it lies close to the periphery of each cell, following all of its individual curvatures (Figs. 2–10), I am convinced that it is not a distinct membrane but only a peripheral layer of clear protoplasm (ectoplasmic layer of Harmer). There is no protoplasmic area in the egg distinct from the yolk, though there is a slight aggregation of protoplasm around the nuclei, but the entire egg is densely packed with small yolk granules which render it opaque.

I have not attempted to study the nuclear phenomena of the maturation and cleavage since the material is very unfavorable for such work. Two polar bodies are formed, the first of which soon after divides (Figs. 1 and 2). These polar bodies do not remain attached to the egg after the sixteen-cell stage, and in some eggs they appear to pass into the cleavage cavity, though in such cases it is difficult to distinguish between polar bodies and small spherules which are cut off from the inner ends of the cleavage cells, and which contain protoplasm and yolk but no nuclei (Figs. 11 and 37). At the stage when the gastrulation begins these spherules are found in considerable numbers in the cleavage cavity (Fig. 37); they disappear in later stages. Similar spherules have been observed by Caldwell ('85) in Phoronis.[1]

The first cleavage is meridional and divides the egg into two slightly unequal blastomeres (Fig. 2); the second cleavage is also approximately meridional and divides each of the blastomeres equally; as a result of this cleavage four blastomeres are formed, two of which are somewhat smaller than the other two (Fig. 4). A polar furrow is present (Figs. 4 and 7) which, taken in connection with the overlapping of certain cells (Fig. 3), indicates that in some eggs at least the cleavage is of a spiral type. The third cleavage is equatorial and leads to the formation of eight blastomeres, all of which are nearly equal in size (Figs. 5, 6, 7); in some eggs the four cells at the animal pole lie just above those at the vegetal pole (Fig. 6); in others they have rotated through various

[1] Quite recently Ideka (1901) has fully described these spherules in Phoronis; he calls them *plasmic corpuscles.*

angles (Figs. 5 and 7). In the eight-cell stage a considerable cleavage cavity appears with openings at the animal and vegetal poles (Figs. 6 and 7).

The cleavage forms just described and represented in Figs. 1–7 are among the most regular ones observed; others are irregular and unequal from the first. One of the most common variations is produced by very unequal divisions, the chief mass of the egg seeming to bud off small cells, usually at the animal pole (Fig. 8). Later stages in which one or two of the blastomeres are much larger than the others, and in which the cleavage cavity is smaller than usual, are not infrequently found. Such eggs appear to give rise to normal blastulæ, in which all the cells are of equal size, by the more rapid division of these larger blastomeres.

The eight-cell stage gives rise to the sixteen-cell stage by the meridional division of each of its blastomeres. Fig. 7 shows each blastomere of the eight-cell stage indented at its periphery, preparatory to this division, which occurs simultaneously in all of the cells. The sixteen cells shown in Fig. 9 and in optical section in Fig. 10 are all of approximately the same size. Except for the occasional presence of the polar bodies at this stage it would be impossible to distinguish the animal from the vegetal pole. The cleavage cavity is now larger and it no longer opens widely to the exterior.

In subsequent cleavage stages division does not take place simultaneously in all of the cells; this is shown, for example, by Fig. 11, in which twenty cells are present, some of which are considerably larger than the others. In the eggs represented in Fig. 12 about forty-eight cells are present and some of these are larger than others, indicating that with them division has been delayed. The egg shown in Fig. 12 has been flattened by the cover glass, so that its apparent diameter is greater than normal; at the same time the blastomeres are separated from one another in an abnormal manner. At all stages the blastomeres are but loosely joined together and they break apart at the slightest pressure. In the later development I have found many embryos which are about one-half or one-quarter the size of the normal embryo, and it seems likely that such embryos have developed from isolated blastomeres of the two- or four-cell stage.

After this brief description of the cleavage, I think it will be quite apparent to everyone that it would be extremely difficult, if

not quite impossible, to work out the cell lineage of *Terebratulina*, even with an abundance of most favorably preserved material. With the material at my disposal such work was wholly out of the question. In the blastula, even at the time when gastrulation begins, one is struck by the great uniformity in size and quality of all the cells. I have found it quite impossible to distinguish any difference between the cells which invaginate and those which do not until after the gastrulation is well advanced.

III. Gastrulation and Formation of Body Layers and Cavities.

Gastrulation occurs by typical invagination, and at the time when the infolding begins there is no difference in the cells at the two poles (Figs. 13 and 37). The infolding continues until the inner layer comes into contact with the outer one and the blastocœl is entirely occluded (Fig. 14 *et seq.*). During this process there is a decided change in the character of the cells of the inner layer; they become very much shorter and henceforth are cuboid or rounded in shape; the cells of the outer layer remain columnar in shape and are very long, so that the ectoderm is quite thick. Large deeply staining granules are found at the free ends of all the cells, both those which are invaginated and those which are not, and in the invaginated cells these granules are so dense that they frequently obscure the nuclei and cell boundaries. In the ectoderm these granules lie on the outer side of the nuclei (Fig. 37 *et seq. Pg*), while the inner ends of the cells are left free from granules and nuclei and hence are very clear. I suggest that these granules may be associated with the cilia, which in life cover the embryo and line the enteron and cœlom (see Morse, '73).

Almost as soon as the inner layer comes into contact with the outer one—*i. e.*, when the infolding is complete—the innermost portion of the archenteron becomes slightly constricted from that portion lying nearer the blastopore. This constriction is deepest anteriorly, least marked posteriorly, while it is about equal on the left and right sides of the archenteron (Figs. 14, 15, 16, 38). On the anterior side this constriction develops into a partition wall, which grows downward and backward into the archenteron, shutting off the enteron above from the enterocœl below (Figs. 16, 20, 42*a* and 42*b*). So far as I am able to determine this partition wall

is always but one cell thick (Figs. 40–42), though in the earlier stages of its development it represents a fold in the wall of the archenteron (Figs. 42*a*–42*b*). The backward growth of this partition wall continues until the enteron is entirely separated from the enterocœl save for a narrow slit-like communication at the posterior end (Figs. 20, 24).

While the enteron is thus being separated from the enterocœl the blastopore is gradually closing and the whole embryo is becoming flattened in a dorso-ventral direction and elongated antero-posteriorly. The blastopore is at first a circular opening; it then becomes narrowed from side to side and apparently elongated antero-posteriorly (Figs. 17–21). The blastopore groove thus formed is shallow posteriorly and deepest at its anterior end where it opens into the enterocœl and enteron (Fig. 17). This groove continues to grow narrower and to be filled up at its posterior end until it becomes a mere slit, opening by a small pore near its anterior end into the enterocœl (Figs. 21, 22). Finally this pore also closes (Fig. 24) and the enterocœl and enteron are completely shut off from the exterior, though still communicating with each other by a narrow opening in the region posterior to where the blastopore closed (Figs. 24 and 46, 47). The blastopore groove persists for some time after the pore has closed but ultimately disappears, though a depression is left at the anterior end of this groove which becomes a part of the anterior mantle furrow; it is probable that at this very point the œsophageal invagination occurs at a stage after the fixation of the larva (see p. 56).

In stages in which the blastopore is still circular the enterocœl is but little larger than the enteron (Figs. 14 and 38). In looking at an entire egg of this stage from the oral side one sees two cavities of about the same diameter, one above the other, which communicate with each other by a wide opening; the cavity nearest the blastopore is the enterocœl, the one nearest the aboral side the enteron. In an older stage (Fig. 17) in which the blastopore has begun to narrow one still sees that these two cavities are of nearly the same diameter. As the enteron becomes separated from the enterocœl, however, the latter becomes much more extensive than the former, and an oral view of an embryo at this stage shows the enterocœl lying on the oral side of the enteron and entirely surrounding it except on the aboral side (Fig. 21, also optical sections, Figs. 19 and 20). This rapid enlargement of the enterocœl

is due in large part to the change in shape of the embryo, which becomes flattened in a dorso-ventral direction and enlarged in its other axes. Associated with the growth of the enterocœl is an important change in the character of its bounding cells; at first they form a quite regular, cuboid or columnar epithelium (Figs. 14–16 and 40–42*a*), but as the enterocœl increases in size the epithelium becomes less regular, particularly at the anterior end, and here many mesenchyme cells come to lie in the cavity of the enterocœl (Figs. 20, 21, 42*b*, 43). Later such mesenchyme cells are found generally throughout most of the cœlom. The cells bounding the enteron remain cuboid or columnar throughout the development.

With the flattening of the embryo and the closure of the blastopore, the ventral wall of the enteron is brought into contact with the ectoderm at the place where the blastopore closes (Figs. 24 and 44–47), and consequently the enterocœl is here divided into right and left cavities, which however still communicate with each other at the anterior end and open into the enteron posteriorly (consult Figs. 43–47 which are transverse sections of an embryo of the stage shown in Fig. 24, Fig. 43 being the most anterior section drawn and Fig. 47 the most posterior). Very soon after this stage the communication between the enteron and the enterocœl is completely cut off and the definitive cœlom is thus formed, consisting of two sacs, still opening into each other anteriorly and posteriorly but separated throughout the middle region of the embryo (consult Figs. 48–52 which are cross sections, in order from the anterior to the posterior region, of an embryo of about the stage shown in Fig. 28).

The gastrulation and formation of body cavities in brachiopods has been observed heretofore only by Kowalevsky. A comparison of the method of gastrulation and cœlom formation in *Terebratulina* with Kowalevsky's observations on *Cistella* and other brachiopods reveals many resemblances and some interesting differences. Kowalevsky found that the gastrula was formed by invagination in *Cistella*, *Terebratula* and probably *Terebratulina*; by delamination or ingression in *Thecidium*. In all cases, however, he describes the cœlom as arising as two lateral pouches from the archenteron in the same manner as in *Sagitta*, viz., by the folding into the archenteron of two lateral partitions. In this way the archenteron is divided into three portions, a median one which becomes the

enteron and two lateral ones which form the cœlom. It is difficult to determine from Kowalevsky's figures from which portion of the archenteron these lateral partitions arise, but there can be no doubt that they are regarded as *folds* of the archenteric wall (see his Fig. 6), nor that they divide the archenteron into three cavities, the enteron and two cœlom sacs. In both of these respects *Cistella* is very unlike *Terebratulina;* in the latter the archenteron is first divided into two cavities and not three (the enterocœl is for a long time unpaired), and the single partition wall by which this division is brought about consists of a single layer of cells and not a plication of the archenteric wall (though in its earliest stages this partition wall probably represents such a plication, Fig. 42*a*). The former of these differences is perhaps not so great as would at first thought appear, being principally due to the fact that in *Terebratulina* the enteron occupies but a small part of the archenteron, and hence the partition wall which separates it from the enterocœl leaves the latter a large unpaired cavity, whereas in *Cistella* the division of the archenteron is more nearly equal and when completed separates two lateral enterocœl pouches from the median enteron. But one cannot overlook the fact that according to Kowalevsky two partition walls are formed in *Cistella*, whereas but a single one is found in *Terebratulina*. Moreover these partitions are lateral in position according to Kowalevsky, whereas in *Terebratulina* the single partition grows out from the anterior wall and merely curves around on to the lateral walls of the archenteron (Fig. 16). The difference in the structure of this partition in *Cistella* and *Terebratulina* is also important; in the former it consists of a double layer of cells, in the latter of a single layer; in *Cistella* the wall of the enterocœl sacs lying next to the enteron becomes the splanchnic layer of the mesoblast, in *Terebratulina* the splanchnic mesoblast is derived from mesenchyme cells. Before attempting to explain these important differences between *Cistella* and *Terebratulina* in the formation of the cœlom it would be well to know that they actually exist, and it seems highly desirable that the embryology of *Cistella* should be reinvestigated with the aid of modern histological methods.

The differences between *Terebratulina* and *Sagitta* in the mode of forming the cœlom are of interest since they remove one important argument for the supposed relationship between Brachiopoda and Chætognatha.

IV. Orientation of the Embryo and Establishment of Definitive Axes.

It is well known that previous investigators of the embryology of the brachiopods have found the proper orientation of the embryo one of their most perplexing problems. The complete closure of the blastopore at a relatively early stage and before many landmarks have appeared by which its position relative to definitive organs could be determined, as well as the fact that both the oral and aboral sides of the embryo are very similar, has been chiefly responsible for this uncertainty of orientation. However if one studies carefully whole embryos of the critical stage when the last remnant of the blastopore is disappearing, the proper orientation of the embryo of a brachiopod is no more difficult than is that of any other animal.

In the stage shown in Figs. 23 and 24 the antero-posterior axis of the embryo is well defined, while the remnants of the blastopore are still present. The enlarged end of the embryo (to the right in Fig. 24) is anterior and gives rise to the head, while the posterior end (to the left in the figure) is narrowed and gives rise to the peduncle. The point where the blastopore closed (Fig. 24, *Br*) lies near the middle of the ventral side, while the blastopore groove runs backward almost to the posterior end of the embryo. Directly opposite the blastopore is a groove which runs transversely across the dorsal side of the embryo; this is the dorsal mantle groove, and the prominent ridge anterior to it is the dorsal mantle fold (Fig. 24, *Md*). If now Fig. 24 be compared with Figs. 20 and 16 it will be seen that the blastopore occupies the ventral-posterior region of the embryo, and that the anterior pole of the embryo is rounded while the posterior pole is pointed, the embryo being flattened on its postero-dorsal side. The prominent ridge opposite the blastopore in Figs. 16 and 20 corresponds with the dorsal mantle fold in Fig. 24. A comparison of these three figures further shows that the axis connecting the middle of the blastopore with the apex of the gastrula invagination (*e. g.*, *E* in Fig. 14) is ultimately bent on itself through an angle of more than 90°. It is difficult to say whether this bending of the gastrula axis is chiefly due to the forward shifting of the blastopore on the ventral side or to the forward shifting of the apex of the gastrula invagination, since there are no points in the embryo which may be

considered as fixed in position. It is highly probable however that both movements occur and that both the apical pole and the blastopore pole are shifted forwards, while the middle of the gastrula axis is shifted backwards, the gastrula axis thus being doubled on itself exactly as is the case in Turbellaria, Annelida and Mollusca. Since the polar bodies have long since disappeared it is impossible to locate exactly on the embryo the point which corresponds to the animal pole of the egg. It is probable, however, that this point lies on the ectoderm directly opposite the apex of the gastrula invagination, and therefore anterior to the ridge which develops into the dorsal mantle fold. In the forward shifting of the apex of the gastrula invagination it is highly probable that this point is also shifted forward and continues to lie opposite the apex of the enteron. If this be true the animal pole of the egg coincides very nearly with the point where the line from *Ce* in Figs. 20 and 24 touches the ectoderm.

The bending of the gastrula axis which has just been described shows that *Terebratulina*, like most bilateral animals, belongs to the group designated by Hatschek ('88) Heteraxonia, and by Goette ('82) Hypogastric forms. Goette has divided bilateral animals into two groups: (1) the pleurogastric, in which the chief axis of the egg becomes the chief axis of the larva or adult, as in *Sagitta* and the echinoderms, and (2) the hypogastric, in which one of the "cross axes" of the egg becomes the chief axis of the larva or adult, as in worms, mollusks and arthropods. There can be no doubt that *Terebratulina* should be classed among the hypogastric forms, and if it be true, which however seems questionable, that *Sagitta* and the echinoderms belong to the pleurogastric type, it shows a very important difference between the embryo of the brachiopod and of the chætognath.

V. Development and Organization of the Larva.

There is of course no natural line of demarcation between the embryo and the larva, but for the sake of convenience we shall designate those stages which precede the closure of the blastopore as embryonic, while those which extend from the closure of the blastopore to the end of the free-swimming life we shall call larval stages.

The flattening of the embryo in the dorso-ventral axis and its

elongation antero-posteriorly have already been described. At the same time the embryo becomes wider at its anterior end and narrower posteriorly. The dorsal mantle groove and fold appear and the fold extends over on to the ventral side of the larva as a slight swelling on each side of the midline (Figs. 25 and 26). These are the halves of the ventral mantle fold and at first they are separated in the mid-ventral line by the blastopore groove (Fig. 26, *Bf*), while the blastopore remnant (*Br*) lies at the anterior end of this groove. Very soon after this stage the halves of the ventral mantle fold fuse with each other, thus obliterating the last trace of the blastopore groove, while a deep notch on the anterior side of the ventral mantle fold (Fig. 29, *O*) represents the place at which the blastopore remnant was last seen.

1. *The Mantle Fold* is at this stage a ring-like prominence which extends all the way around the larva (Figs. 29, 30, 31). This ring passes obliquely around the larva, being nearer the anterior end on the dorsal side and nearer the posterior on the ventral side (Fig. 31). Two mantle furrows are now plainly distinguishable, one in front of and the other behind the mantle fold. The anterior furrow is deepest on the ventral side, while the posterior one is deepest on the dorsal side (Figs. 29–31). With the appearance of the mantle, bounded anteriorly and posteriorly by these constrictions, the mantle furrows, three regions may be recognized in the larva, viz., the cephalic region, in front of the anterior mantle furrow, the mantle, between the anterior and posterior furrows, and the peduncular region, behind the posterior mantle furrow.

These constrictions, which I have called the anterior and posterior mantle furrows, continue to grow deeper but at no time do they form true septa which divide the cœlom. The regions which they separate are not, therefore, segments, as Kowalevsky supposed. The larva is at this, and all other stages which I have studied, unsegmented, and the appearance of segmentation is due merely to the formation of the mantle from the middle region of the body.

The mantle becomes a very prominent ring around the body, and then its free edge is turned backwards until it surrounds the peduncular regions on all sides (Figs. 32–36). A space is left between the mantle and the peduncle which is the peduncular chamber (Figs. 34 and 36, *PC*). This chamber is a little deeper and wider on the dorsal than on the ventral side, which is due to the fact

that the posterior mantle furrow is deeper and is farther forward on the dorsal than on the ventral side (Fig. 31, *Fp*).

When the mantle has reached the limit of its backward growth it entirely covers the peduncle, the extremity of which nearly fills the circular opening of the mantle chamber (Figs. 34 and 36). This is the oldest stage which I have had opportunity to study. Morse ('71) has observed in detail the transformation of this larva into the adult. He figures a great many stages showing the manner in which the mantle is turned forward over the cephalic region, its free edge being directed forward and its originally internal surface becoming external. This happens after the larva has become fixed by the tip of its peduncle, and it is evident from Morse's figures and descriptions that the stage shown in my Figs. 34–36 is one of the last stages in the free-swimming life.

2. *The Cephalic Region* lies in front of the anterior mantle fold and is nearly hemispherical in shape, being however somewhat variable in form (consult Figs. 32–36), which is probably due to the fact that it is extremely contractile, as Morse has observed. At its anterior end and slightly toward the dorsal side is a shallow depression, the apical sense plate, which bears a tuft of long cilia in life (see Morse). The enlarged end of the enteron as well as a portion of the mesoderm and cœlom extend into the cephalic region.

3. *The Peduncular Region* is cylindrical in shape and is contracted near its posterior end. This contraction is due to the fact that the cœlom and mesoderm terminate abruptly some distance in front of the end of the peduncle (Figs. 34 and 36), and it is certainly not to be taken as constituting a fourth region of the larva, as Shipley ('82) suggests in the case of *Cistella*. The endoderm is continued as a solid cord of cells nearly to the end of the peduncle.

4. *The Ectoderm* covering the larva is unusually thick, though consisting of but a single layer of cells; these cells are however extremely long. Their inner ends are clear and free from nuclei and granules, so that on first examination a clear zone seems to separate the outer from the inner layer (Figs. 38 *et seq.*). Only on the anterior side of the mantle fold does the ectoderm become cuboid or squamous, while over the cephalic and peduncular regions it is particularly thick.

5. *Setæ Sacs.*—High columnar cells line the peduncular chamber,

and at four places (two median and two lateral) on the dorsal side of the mantle the epithelium is invaginated to form the setæ sacs (Figs. 34, 36, 56–64, *SS*). No traces of setæ are preserved in the material which I have examined, but there can be no doubt from Morse's ('73) account that these invaginations give rise to the lateral and median bundles of temporary setæ.

6. *Sense Plates and Ganglia.*—A little toward the dorsal side of the apex of the cephalic lobe is a depression in the ectoderm, and in this region the cells are deeply pigmented, especially at their free borders. This is the apical sense plate (*Scheitelplatte*) (Figs. 26, 28, 29, 31, 32, 34, 35, 36, 56, 57, 58, *CG*), and in life bears a tuft of long cilia (see Morse, '73), though no trace of these is left in the material which I have examined. At the base of the cells of this sense plate ganglion cells are cut off from the epithelial cells, but continue to lie in the ectoderm (Figs. 28, 36, 56, 57). These ganglion cells are small and I have been unable to observe their further development, but there seems no reason to doubt that they represent the cerebral ganglion.

A similar sense plate and ganglion is formed on the midventral line immediately posterior to the place where the blastopore remnant closed and in the region where the blastopore lips fused along the mid-line (Figs. 29, 31, 35, 58, 61, 62, *SG*). This is the ventral sense plate, and the cells of this plate are pigmented as are those of the apical plate; I think it probable that they bear a tuft of long cilia in life, although no one has observed this feature as yet. As in the case of the apical plate, ganglion cells are cut off from the basal ends of the epithelium of the ventral plate, and here again there seems every reason to believe that these ganglion cells become the subœsophageal ganglion. The œsophagus has not formed in the oldest larva which I have been able to study, but a slight invagination of the ectoderm immediately anterior to the ventral sense plate probably represents the earliest step in the formation of the œsophagus (Fig. 58, *O*). Heretofore no observations have been made on the early development of the nervous system. Neither Morse nor Kowalevsky observed any stages in the formation of the nervous system. Shipley has observed in the head region of *Cistella* a small clump of cells without granules, which he suggests may be a nerve ganglion; his Fig. 35 shows however that it lies entirely within the mesoderm, and it cannot therefore be a ganglion. Brooks has described in detail the nervous system of the larva of

Glottidia, but this system is already well formed in the earliest larva which he observed.

7. *Enteron.*—The cavity of the enteron is flask-shaped, the enlarged end lying in the cephalic region while the pointed extremity extends into the peduncle. In early larval stages the transverse diameter of the enteron is greater than its dorso-ventral diameter (Figs. 25 and 44–50); in later stages it becomes circular in cross section (Figs. 53–55), while in still later stages it becomes compressed laterally so that its greater diameter is in a dorso-ventral direction (Figs. 33, 35, 56–60). In the oldest stages which I have observed a diverticulum from the anterior end of the enteron grows out toward the ventral side, and at the same time an invagination of the ectoderm appears in the anterior mantle furrow, at the very point where the blastopore remnant disappeared, and grows in toward this diverticulum (Figs. 35 and 58). I presume that this is the first step in the formation of the œsophagus. During the whole of the larval period the enteron has no opening to the exterior. According to Morse ('73) the mouth is formed late in the metamorphosis, and while he does not describe the place or manner of its formation his Fig. 90 shows it at the anterior extremity of the young brachiopod. Kowalevsky ('74) also has described and figured what he considers to be the formation of the œsophagus at the anterior end of the cephalic lobe. From what I have observed I feel confident that the mouth is first formed on the ventral side, in the region of the anterior mantle furrow, and if it is later found at the anterior end of the young brachiopod, its change in position must have been brought about by secondary changes. Kowalevsky expresses some doubts as to whether the invagination observed by him at the anterior end of the cephalic lobe is really the œsophagus, and from its location I would suggest that it is the apical sense plate and cerebral ganglion rather than the œsophagus. My observation as to the location of the stomodæal invagination thus confirms Heider's ('93) theoretical suggestion and brings the brachiopod larva into close relationship with the trochophore.

The cells bounding the lumen of the enteron are cuboid in early stages and columnar in later ones (compare Figs. 43–50 with Figs. 56–60). These cells, enclosing a minute lumen, extend through the entire peduncular region (Figs. 36, 57, 58, 61–64).

From its earliest formation the enteron is in contact on its dorsal

side with the ectoderm, while laterally and on its ventral side it is bounded by mesoderm (Figs. 43–52, 58 and 61–63).

8. *Cœlom.*—For a long time after the division of the cœlom into right and left cavities by the flattening of the embryo and the closure of the blastopore these sacs communicate with each other both anteriorly and posteriorly (Figs. 43–47, 48–52, 53–55). In still later stages these communications are closed by the practical elimination of the cœlom in the cephalic and peduncular regions through the proliferation of mesenchyme cells (Figs. 56–63). The cœlom sacs, which are at first of nearly the same size both anteriorly and posteriorly (Fig. 25), become much constricted in the peduncular region while they still remain large in the head and mantle regions (Fig. 26). In the latter region they then become lobulated, often showing a trefoil condition (Figs. 27, 28), and with the further development of the dorsal and ventral mantle folds a lobe of the cœlom is sent into each of these folds (Figs. 29–33). At the same time the cœlom in the cephalic and peduncular regions grows smaller, while that in the mantle grows larger. Finally almost the entire cœlom is contained in the mantle, the portion in the head and peduncle being very small (Figs. 36 and 56–63). The posterior limits of the peduncular cœlom is marked by a narrowing of the peduncle, which probably represents the fourth "segment" of Shipley. The cœlom however is never segmented though it may be constricted in certain places. The constrictions shown in Figs. 27–31 are quite constant in position and are connected with the extension of the cœlom into the mantle lobes, but they never coincide in position with the superficial constrictions of the body (mantle furrows). In a few abnormal larvæ of the stage shown in Fig. 25 I have found each cœlom sac partially divided by mesenchyme cells into three cavities. That these divisions, however, have no real importance is shown by the fact that their number differs in different larvæ and is sometimes different on opposite sides of the same larva.

In the early larval stages the enteron is in close contact with the ectoderm on the dorsal side, while a collection of mesoderm cells on the ventral side of the enteron separates the two cœlom sacs and may be considered the rudiment of a ventral mesentery (Figs. 49, 50).

In later stages the cœlom is almost entirely obliterated, except in the mantle, and consequently the enteron is surrounded by

a dense mass of mesoderm cells, except on the dorsal side, where it is still in contact with the ectoderm (Figs. 56–64). At this stage therefore there can be no mesenteries since there is practically no cœlom.

In early stages of larval life the mesoderm cells are mesenchymatous in the anterior region of the body and epithelial in the posterior regions (*cf.* Figs. 43–46). In the later stages the mesoderm cells of the posterior regions become more mesenchyme-like (Figs. 48–52 and 53–55), while in still later stages they become densely packed and pigmented and it is impossible to distinguish their cell boundaries (Figs. 56–64).

VI. General Considerations and Conclusions.

Although I am not one of those who expect to find phylogeny "writ large" in ontogeny, yet it may be worth while to point out the bearings of the development of *Terebratulina* on the supposed relationships of brachiopods. Since my own studies cover only the embryonic and larval periods, I shall of course limit to those periods the comparison of *Terebratulina* with other forms. Within these periods we may compare (1) the cleavage, (2) mesoderm and cœlom formation, (3) orientation of embryo and larva, (4) the general morphology of the larva.

1. *The Cleavage.*—As has been said already, there is no evidence that the cleavage of *Terebratulina* resembles that of mollusks or annelids. It is now known that in a great many annelids and leeches and in all groups of mollusks except the cephalopods the cleavage is of a certain determinate or morphogenetic (Child, 1900) type. The principal characteristics of this type of cleavage are that the ectoderm is segregated in three quartettes of cells, that the greater part of the mesoderm appears in one cell (4d) of the fourth quartette, and that the remaining cells of the fourth quartette together with the basal cells (macromeres) constitute the endoderm, and finally that the elongation of the embryo takes place by the teleoblastic cleavage of certain cells in the ectoderm and mesoderm (first and second somatoblasts, 2d and 4d) and possibly also in the endoderm (endodermic derivations of 4d). In addition to these general characteristics of the cleavage of annelids and mollusks there are other characteristics less general in application, such as the derivation of the prototroch, the stomodæum, the cerebral

ganglia, etc., from certain cells of the ectoderm. Wilson ('99) has shown that many of the general characteristics mentioned above are applicable also to the cleavage of the Turbellaria.

With regard to some of these general characteristics it is impossible at present either to affirm or deny their presence in *Terebratulina*. For example, owing to the difficulty of identifying individual cells I cannot say whether or not the ectoderm is segregated in three quartettes. In fact I am wholly unable to recognize quartettes at all after the eight-cell stage. It is certain, however, that the mesoderm is not formed by teleoblastic growth from a single cell and that the embryo does not grow in length by the teleoblastic cleavage of two somablasts. Furthermore the cleavage of *Terebratulina* shows no resemblance to any type of determinate or morphogenetic cleavage which has yet been described, whether among annelids, mollusks, turbellarians, nematodes or ascidians. On the other hand it does resemble in some respects the indeterminate cleavage of echinoderms, Phoronis and ectoproctous Bryozoa.

2. *Mesoderm and Cœlom.*—The gastrulation occurs by typical invagination; however, this method of gastrulation is found in almost every great group of animals, and therefore no phylogenetic significance can be attributed to it. In the formation of the cœlom however the case is somewhat different. The method of mesoderm and cœlom formation in *Terebratulina* is totally unlike that which is found in annelids, mollusks, platyhelminths, nematodes and arthropods, while it shows certain resemblances to chætognaths and echinoderms. A more detailed comparison shows however that even these resemblances are not very close.

In echinoderms the enterocœl is formed at the inner end of the archenteron, while the enteron arises from that portion of the archenteron nearest the blastopore; in brachiopods the enteron is formed from the inner end of the archenteron, while the enterocœl arises from that part of the archenteron which in echinoderms gives rise to the enteron. It is evident therefore that no real resemblance exists between echinoderms and brachiopods in this respect.

In chætognaths the method of cœlom formation is more like that in brachiopods—in fact Kowalevsky supposed that the two were identical—and yet there are important differences here also. In *Sagitta*, according to both Kowalevsky ('71) and Hertwig ('80), two bilateral folds of the archenteric wall grow into the archen-

teron from its apex, thus dividing the cavity into a median one, the enteron and two lateral ones, the enterocœls. The stomodæum is said to open into the apical end of the enteron, directly opposite the blastopore, which has however closed at an earlier period. In *Terebratulina*, on the other hand, the enteron is separated from the single enterocœl by one partition which grows out from the anterior wall of the archenteron and divides the latter into a dorsal cavity, the enteron, and a ventral one, the enterocœl; only later, by the closure of the blastopore and the flattening of the embryo, does the enterocœl become divided through its middle region into right and left cavities, which, however, continue for some time to communicate with each other both anteriorly and posteriorly. Moreover the stomodæum in *Terebratulina* is formed in the position of the former blastopore and not on the opposite side of the embryo. Therefore, although there are certain general resemblances between the two, I cannot regard the cœlom formation in chætognaths and brachiopods as being more than analogous processes, and as such devoid of phylogenetic significance.

In *Phoronis*, according to Caldwell ('85), two pairs of cœlomic cavities are formed by a modified type of enterocœl formation, which however bears no resemblance to that in *Terebratulina*. The anterior one of these cavities gives rise to the cavities of the epistome and lophophore, the posterior one to the chief body cavity.

Masterman's (1900) work on the development of *Phoronis* furnishes the most complete account of the early development of this interesting form which has yet been given.[1] In an earlier work ('97) he found that there were three separate and distinct cœlomic cavities in the larva, a preoral or epistomal cavity, a collar or lophophoral cavity and a trunk cavity. In his later paper he describes the origin of these cavities; the first of these arises as a median outgrowth from the anterior side of the archenteron, the other two arise as paired masses of solid mesoderm cells in which cavities appear later. In the matter of the formation of the anterior or procœlomic cavity there is much resemblance between *Phoronis* and *Terebratulina*, but in the latter animal the mesocœlomic and metacœlomic cavities are entirely absent.

[1] Since the appearance of Ideka's (1901) work this statement is no longer true. Ideka has given by all odds the most complete account of the embryology of Phoronis yet published. (See postscript, p. 70.)

Very little is certainly known of the formation of the mesoderm and cœlom among the Bryozoa. In the Ectoprocta the larval form is usually solid, the cœlom and enteron having undergone extensive if not complete degeneration, while in those forms in which the cœlom is still preserved its method of origin is highly peculiar. For example, in the Phylactolæmata the central cavity of the embryo is generally considered to be the cœlom, although at the stage at which it appears there is neither endoderm nor enteric cavity in the embryo (see Korschelt and Heider's Text-Book).

Among the Endoprocta the mesoderm arises in *Pedicellina*, according to Hatschek, from two pole cells which appear at the posterior edge of the blastopore; these cells by repeated divisions give rise to two short mesoderm bands, and from these bands mesoderm cells arise which fill the space between the ectoderm and the endoderm. It appears therefore that no direct comparison can be made between *Terebratulina* and the Bryozoa in the matter of the formation of mesoderm and cœlom.

3. *Orientation of Embryo and Larva.*—As has been pointed out already the relation of the chief axis of the gastrula to the chief axis of the larva is the same as is found in all Heteraxonia (Hatschek) or Hypogastric forms (Goette). The animal pole of the egg and the apical pole of the gastrula become the cephalic pole (*Hirnfeld*) of the larva, while the blastopore comes to lie on the ventral side. Such a relation of the embryonic and larval or adult axes is of very general occurrence, being found at least in all Trochozoa (Hatschek). Moreover in having a blastopore which becomes narrow from side to side and then closes from behind forward, and also in the formation of the stomodæum at the place where the blastopore closed, *Terebratulina* agrees with a large number of bilateral animals belonging to widely different phyla. These characters are so general, therefore, as to be of little value in determining the affinities of the brachiopods. Regarding the apical sense plate as anterior and the subœsophageal sense plate as ventral in position, it follows that the peduncle is posterior and the mantle folds dorsal and ventral; consequently even after the metamorphosis the peduncle is posterior, and the valves which are formed by the mantle folds are dorsal and ventral, while the opening of the valves is anterior. This orientation is the commonly accepted one and is directly opposed to Caldwell's ('82) remarkable views, according to which both valves and the peduncle are ventral in position.

4. *General Morphology of Larva.*—The resemblances between the early embryos of *Terebratulina* and those of other metazoa are so general in character that they afford little assistance in determining the affinities of the brachiopods. We must therefore rely largely upon the structure of the larva and of the adult for the solution of this problem.

(a) *Comparison with Trochophore.*

Among the chief characteristics of the trochophore larva, as enumerated by Hatschek ('88, p. 307), are the following:

I. (1) Bilateral symmetry, (2) mouth on ventral side, (3) anus near posterior end, (4) shape ovoid.

II. (5) Apical tuft of cilia, (6) preoral ciliated band (Trochus), (7) postoral ciliated band (Cingulum), (8) adoral ciliated zone, (9) ventral ciliated furrow between mouth and anus, (10) small cilia over general surface of larva.

III. (11) Epithelial nervous system, (12) apical plate (*Scheitelplatte*), ganglion and sense organs, (13) œsophageal nerves and buccal (ventral) ganglion, (14) ventral (and sometimes dorsal) longitudinal nerves.

IV. (15) Alimentary canal (œsophagus, stomach and intestine) horseshoe-shaped and ciliated throughout, (16) stomach retort-shaped, (17) intestine reaches to posterior end of body.

V. (18) Mesoderm partly mesenchymatous, partly epithelial, (19) mesenchyme gives rise to branched connective tissue cells and thread-like or branched muscle cells, (20) ventral and dorsal longitudinal muscle pairs, (21) preoral and postoral ring muscles, (22) dilatators and constrictors of œsophagus and intestine, (23) mesothelium gives rise to the paired protonephridium, which is a longitudinal ciliated tube closed at the anterior end by terminal cells, and opening posteriorly on the ventral side in front of the anus, (24) paired cœlomic sacs at the posterior end.

Of these characteristics, numbers 5, 6, 7, 8, 11, 12, 13, 15, 16, 17 and 23 are undoubtedly the most important, and all of these except the last are found also in brachiopod larvæ. All investigators of the embryology of brachiopods have described the apical tuft of cilia (5); the preoral ciliated band (6) is probably

represented in the brachiopod larva by the circle of longer cilia found at the base of the preoral lobe (see Kowalevsky's figures of *Argiope* larvæ); the postoral ciliated band (7) is probably represented by the mantle, which attains a much greater development in the brachiopod larva than in the ordinary trochophore; the adoral ciliated furrow (8) is represented by the anterior mantle furrow; the fact that adult brachiopods have an epithelial nervous system (11) has long been known, and I have observed the beginnings of such a nervous system in the larva of *Terebratulina;* I have also observed (p. 55) the apical plate and ganglion (12) and the ventral plate and ganglion (13) in *Terebratulina;* only the beginnings of the œsophageal invagination are shown in the oldest larva which I have studied, but it is evident from its position that after it joins the stomach the alimentary canal will be horseshoe-shaped (15); the stomach in *Terebratulina* larvæ is retort-shaped (16) and the intestine reaches to the posterior end of the larva (17).

In addition to these more important characteristics the larvæ of *Cistella, Thecidium* or *Terebratulina* agree with the trochophore in the possession of the following characteristics: Bilateral symmetry (1), blastopore and *anlage* of mouth on ventral side (2), ventral blastopore groove (9) and general ciliation of body (10), mesoderm partly mesenchymatous, partly epithelial (18); finally ventral and dorsal longitudinal muscles (20) are present in the peduncle of *Cistella.* These brachiopod larvæ also agree with many chætopod larvæ in the possession of ectodermal seta sacs and provisional setæ.

The points in which the larvæ of testicardinate brachiopods differ most from the trochophore are in the absence of mouth and anus and the lack of a protonephridium. In the Ecardines however both mouth and anus are present during larval life, and in all brachiopods a single pair of nephridia appears after the larval period. The absence of these larval structures therefore indicates a retardation or less perfect development of the larval brachiopod as compared with the typical trochophore. I believe therefore that the brachiopod larva belongs unquestionably to the trochophore type.

(b) *Comparison with Actinotrocha.*

The larva of *Phoronis,* while showing many peculiarities, bears a most decided resemblance to the trochophore. Among its principal characteristics may be enumerated the following:

I. (1) There are three sections of the body: (a) the preoral lobe, (b) the postoral section (collar) which carries tentacles, and (c) the posterior or anal section (trunk); (2) the preoral lobe probably represents the umbrella of the trochophore; (3) the cilia at its margin probably correspond to the preoral ciliated band (Trochus), while (4) the postoral ciliated zone (collar) which carries the tentacles probably corresponds to the postoral band (Cingulum) of the trochophore; (5) this postoral ciliated zone (Cingulum) runs obliquely around the body, being further posterior on the ventral than on the dorsal side; (6) tentacles appear near the ventral midline and fresh pairs are added dorsally.

II. (7) There is an epithelial nervous system, (8) an apical plate, ganglion and (in some species) eye spots, and (9) an œsophageal commissure.

III. (10) The cœlom is composed of an anterior unpaired cavity and two pairs of cavities posterior to this (Masterman);[1] (11) the anterior cœlom sac arises as an enterocœl, the posterior paired ones as schizocœls; (12) there is one pair of protonephridia, which end blindly internally in connection with excretory cells.

IV. (13) There is a ventral invagination posterior to the zone of tentacles and a peculiar metamorphosis by the evagination of this invagination; (14) during metamorphosis the tentacles turn forward, and (15) the anus comes to lie on the dorsal side of the mouth, the intestine thus forming a loop.

Comparing now the larvæ of brachiopods with the Actinotrocha we find that, in addition to the general resemblances to the trochophore which both show, there are the following special resemblances between the two: (1) In both brachiopods and Actinotrocha the postoral ciliated zone (Cingulum) is greatly enlarged and runs obliquely around the body, being farther posterior on the ventral than on the dorsal side. (2) In both cases this forms the mantle or lophophore, though the tentacles or cirri which are borne upon it appear much earlier in Actinotrocha than in the brachiopod larva. (3) Brooks has shown that in Lingula the ventral pair of

See postscript, p. 70.

tentacles appears first and that successive pairs of tentacles are added dorsally, exactly as in Actinotrocha. (4) In the metamorphosis the mantle (lophophore) is turned forward over the preoral lobe in exactly the same way in both cases. These are extremely important resemblances, and in themselves lend support to the view that *Phoronis* and the Brachiopoda are closely related.[1]

On the other hand, according to Masterman's ('97 and 1900) recent work on Actinotrocha, there are certain important respects in which Actinotrocha differs decidedly from the brachiopod larva: (1) The cœlom consists of an anterior unpaired cavity and of two pairs of cavities, one of which lies in the lophophore and the other in the trunk region. The anterior unpaired cavity somewhat resembles in position and method of origin the anterior portion of the enterocœl of *Terebratulina*, but the lophophoral and trunk cavities of Actinotrocha differ from the mantle and peduncular cœlom of *Terebratulina* in that the latter are a part of the enterocœl and are never completely separated from one another, whereas in Actinotrocha they arise as schizocœls and are always separate. (2) Actinotrocha also has rudiments, at least of a second pair of nephridia. (3) It also has two endodermal outgrowths from the anterior portion of the enteron, which are composed of large vacuolated cells, and are homologized by Masterman with the notochord of the Hemichorda.[2]

I have had no opportunity of studying the later stages in the development of the brachiopod, in which alone the two last-mentioned structures might be looked for, and cannot therefore determine whether there are real differences between the brachiopod and *Phoronis* in these respects. With regard to the differences shown by the cœlom, one must bear in mind the fact that in the brachiopod larva the cœlom almost entirely disappears, except in the mantle, and a segmentation of the cœlom in later stages could not therefore be observed, even if it had at one time existed in the ancestors of the brachiopods. There can be no doubt however that in *Terebratulina* the entire cœlom arises from a single enterocœl, in which respect there is a decided difference between the brachiopod and *Phoronis*. The resemblances mentioned above

[1] The presence of "plasmic corpuscles" (Ideka, 1901) in the blastocœl of both forms is another interesting resemblance (see p. 45).

[2] See postscript, p. 70.

however are so important and extend to such details that I am inclined to accept the view that *Phoronis* and the Brachiopoda are related, and to look to future work on the development of both of these groups to harmonize the apparent differences between them.

(c) *Comparison with Larval Polyzoa.*

Brooks in particular has emphasized the resemblance between the larvæ of Polyzoa and Brachiopoda, basing this comparison, however, rather upon the external characters in which both resemble the trochophore than upon a detailed comparison of internal structure.

Ectoprocta.—It is extremely difficult to compare larval brachiopods with larval ectoprocts, owing to the great variety of forms presented by the latter, their many secondary characters, and the conflicting accounts of their structures and homologies which have been given by various authors. There is some reason for believing however that the ectoproct larva belongs to the trochophore type, and that the following parts of the two may be homologous: (1) The retractile disk may correspond (at least in part) to the apical plate, (2) the corona in part to the trochus, (3) the sucker to the trunk of the trochophore, or to the ventral evagination of Actinotrocha. Furthermore one may trace a certain resemblance between the invaginated sucker of *Bugula* and *Lepralia* and the peduncle and mantle of *Terebratulina*. In both cases attachment takes place by the peduncle, while the covering folds (mantle in the case of brachiopods) are turned forward as the peduncle is protruded. However the degeneration and modification of structures, both in the larval stages and in the metamorphosis, are so extreme that any attempt at the present time to trace homologies between larval Ectoprocta and other forms must be accompanied by a lively imagination and a ready facility in guessing.

There is good evidence in the degeneration of the intestine and cœlom of the ectoproct larva, and in the general degeneration which accompanies its metamorphosis, that we are dealing with a highly modified type of development, which is little likely to throw light upon the affinities of the Polyzoa. However the resemblances between the adult Polyzoa and Phoronis and the Brachiopoda is such as to warrant the conclusion that these groups are at least remotely related to one another.

Entoprocta.—Among larval entoprocts there are few, if any, undoubted homologies with either the trochophore, the actinotroch,

or the brachiopod larva. It is possible that the ciliated disk of *Pedicellina* and *Loxosoma* is homologous with the retractile disk of the ectoproct larva and with the apical plate of the trochophore, and that the margin of the vestibule (ciliated ring) in the former corresponds to the trochus of the latter, but these possible homologies are too hypothetical to be affirmed with any degree of assurance.

5. *Conclusions.*—Neglecting the older views as to the affinities of the brachiopods with lamellibranchiate Mollusca, which were founded merely upon superficial resemblances, we find that within recent times the brachiopods have been associated, at different times and by different authors, with Chætopoda, Polyzoa, Chætognatha and Phoronis.

Both Morse ('73[2]) and Kowalevsky ('74) independently reached the conclusion that the brachiopods are chætopod annelids. Morse says in summing up his work on the subject ('73[2], p. 57): "We must regard the brachiopods as *ancient cephalized chætopods*, while *Serpula*, *Amphitrite*, *Sabella*, *Protula* and others may be regarded as *modern* (later) *cephalized chætopods*"; and Kowalevsky ('74) maintained that the brachiopods ought to be considered simply as an order of the annelids, which present at least as many resemblances to the chætopods as do the leeches.

Morse has enumerated twenty-four characteristics in which brachiopods resemble more or less closely Vermes, sedentary annelids and Gephyreans. Kowalevsky also names a considerable number of points in which brachiopods resemble chætopods. Some of these features are not actually characteristic of the brachiopods, as, for example, the segmentation of the larva; others are of such a general character as to apply to almost all Bilateralia, as Brooks has shown, while still others represent real resemblances between the brachiopod larva and the trochophore. The trochophore larva however is of such wide occurrence among bilateral animals, that the mere classification of the brachiopods among the Trochozoa throws no light upon the nearer affinities of this group.

Huxley, Lankester, Claus and others have regarded the brachiopods as more or less closely related to the Polyzoa, and Brooks in particular has held that the two groups belong to the same phylum and class. "The organization of the *Lingula* larva," he says, "shows that it is not merely like a Polyzoon, but that it actually is one; as much so as the hydra stage of an Hydro-Medusa is a

Hydra, or the tailed larva of Botryllus is an Appendicularia, and more so than a tadpole is an urodellan Batrachian." This close relationship he bases largely upon the external resemblances between the larvæ of *Thecidium* and various Polyzoon larvæ. It seems to me that some of these resemblances are real homologies, but on the other hand the differences between these larvæ, as well as between the adults of these two groups, are so great that it would be inadvisable to place them together in the same class; though I believe they should be placed in the same phylum. Moreover it seems to me that Brooks' view, that the Polyzoa are the ancestral form of which the Brachiopoda are a specialization, is just the reverse of the real relationship; larval as well as adult Brachiopoda show less specialization and certainly less degeneration than the Polyzoa.

The resemblances of the brachiopod larva to the Molluscan veliger, upon which Brooks lays emphasis, are in the main the same as the resemblances to the trochophore, the veliger and trochophore belonging to the same type of larva.

The idea that the brachiopods are related to the chætognaths, which was suggested by Bütschli and Hertwig ('80) and maintained by van Bemmelen ('83), has little more in its favor than the supposed resemblance in the method of formation of the cœlom and in certain histological details.

So far as the formation of the cœlom is concerned, I have already pointed out the fact that in *Terebratulina* it forms in a very different manner from what obtains in *Sagitta*, and as for the histological resemblances they are by no means confined to the two groups in question. On the other hand there are so many important differences between the two groups, both in their embryology and in their adult structure, that one could as well maintain the affinity of the Brachiopoda with Echinodermata, Enteropneusta or Chordata, as with Chætognatha.

Caldwell ('82) first pointed out in detail the resemblances between *Phoronis* and the Brachiopoda. In this paper he has urged "an entirely new view of the homologies of the body surfaces in Brachiopoda." He regards the Brachiopoda as fixed by their ventral surface, and both valves of the shell as ventral in position, the peduncle of the brachiopod corresponding to the ventral invagination of Actinotrocha. While there are some facts which may be urged in favor of this view there are many which may be used

against it. The fact that in both *Phoronis* and *Lingula* the intestine forms a loop, the anus opening near the mouth, and that fixation takes place by the posterior extremity, has led to Caldwell's view as to the homologies of the body surfaces in the brachiopods. On the other hand the ventral mantle fold of *Terebratulina* forms directly across the region where the blastopore lips fused and immediately posterior to the place where the blastopore remnant closed and where the mouth later appears. Upon the anterior face of this fold the subœsophageal sense plate and ganglion appear; there can be no doubt therefore that this fold is ventral in position. The dorsal mantle fold appears at a very early stage (Figs. 16 and 20) on the apical side of the gastrula and just posterior to the chief gastrula axis; it is impossible therefore that it should be considered as ventral in position. *Furthermore the mantle folds of the brachiopod correspond to the zone which bears the tentacles in Actinotrocha* (collar, Masterman) *and not to the margins of the ventral invagination;* and since the mantle folds surround the body posterior to the mouth, both of them cannot be ventral in position. Whether the peduncle is ventral or not cannot perhaps be determined with certainty until we know the embryology of a brachiopod in which the anus and terminal portion of the intestine are present. In *Lingula*, as is well known, the anus opens near the mouth and on the left side; in *Crania* it is terminal in position, and the embryology of either of these forms should throw light on this question as to the morphological position and homologies of the peduncle. Brooks' work on *Lingula* deals only with stages in which the anus and the intestinal loop are already present, and one cannot therefore tell at what point relative to the blastopore the anus appears and how the loop is formed. It is certain however that the ventral invagination and remarkable metamorphosis of Actinotrocha are cœnogenetic rather than phylogenetic characteristics, and that parallel phenomena need not be expected in other groups of animals. Furthermore it is certain that the peduncle in *Terebratulina* is derived from that portion of the gastrula which is posterior to the blastopore; I do not see therefore how it can be regarded as ventral in position. But however this problem of the relation of the peduncle of the brachiopod and the ventral invagination of Actinotrocha may be decided by future work, it seems to me that the affinities of *Phoronis* and Brachiopoda are well established. I agree therefore in the main with the views of Caldwell, Lang and Blochman, and

more particularly with the position of Heider, as to the affinities of the brachiopods. The relationship between Phoronis, Bryozoa and Brachiopoda seems to me sufficiently close to justify the placing of them in the same phylum, though not in the same class, as Lang has done.

Postscript.

Since this paper was written I have seen Ideka's (1901) very important contribution on the "Development, Structure and Metamorphosis of Actinotrocha." Ideka's work is in all respects the most thorough and extensive which has yet been done on the development of Actinotrocha, and in many very important points he differs decidedly from Masterman. Some of the differences between Actinotrocha and the brachiopod larva, which are pointed out on p. 65, disappear in the light of this work. For example, Ideka finds that there is but one complete septum in the body, that between the collar and the trunk, while the cavities of the preoral lobe and collar are in communication through a very incomplete septum. Furthermore Ideka finds no trace of a second pair of nephridia or of a "proboscis pore," such as Masterman described, while the two "chorda" diverticula of Masterman (Diplochorda) are represented by a single unpaired diverticulum in the Japanese species. Whether this is a glandular or skeletal structure is left an open question.

With the exception then of the single septum between the collar and the trunk regions there are no important differences between Actinotrocha and the brachiopod larva. This septum occupies a position in Actinotrocha corresponding to the posterior mantle furrow of the brachiopod larva, and it would be interesting to know whether, in stages of the brachiopod larva later than those which I have studied, any trace of a septum can be found in this position.

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REFERENCE LETTERS.

Bc, Blastocœl.
Bf, Blastopore groove.
Bp, Blastopore.
Br, Blastopore remnant.
C, Cœlom.
Ce, Enterocœl.
Cc, Cephalic Cœlom.
Cm, Mantle Cœlom.
Cp, Peduncular Cœlom.
Ccm, Cephalic and Mantle Cœlom.
Cmd, Dorsal extension of Mantle Cœlom.
Cmv, Ventral extension of Mantle Cœlom.
CG, Apical Sense Plate and Cerebral Ganglion.
D, Dorsal.
DA, Dorsal-Anterior.
E, Enteron.
Em, Egg Membrane (ectoplasmic layer).
Fa, Anterior Mantle Furrow.
Fp, Posterior Mantle Furrow.
Ge, Gastrocœl.
M, Mantle.
Md, Dorsal Mantle Fold.
Mv, Ventral Mantle Fold.
mc, Mesenchyme.
O, Point where blastopore closed and œsophageal invagination appears.
P, Peduncle.
Pb, Polar Bodies.
PC, Peduncular Chamber.
Pg, Dark Staining Granules.
SG, Ventral Sense Plate and Sub-œsophageal Ganglion.
SS, Setæ Sacs.
V, Ventral.
VP, Ventral-Posterior.

Description of Figures.

All the figures illustrating this paper were drawn with Camera Lucida at the stage level under a Zeiss Apochromat. Homog. Immers. Obj. 3mm. Comps. Occ. 4. In the process of reproduction they have been reduced about one-third.

Plate I.

Fig. 1. One-cell stage; polar body in process of being formed; egg elliptical; ectoplasmic layer surrounds egg and polar body.

Fig. 2. Two-cell stage; one cell larger than the other; three polar bodies present.

Fig. 3. Transitional stage between two-cell and four-cell stages; showing overlapping of certain cells and "spiral" character of cleavage.

Fig. 4. Four-cell stage, two cells (at right) larger than the other two; protoplasmic areas surrounding nuclei shown; two polar bodies lie in the polar furrow.

Fig. 5. Eight-cell stage, apical view; three polar bodies at animal pole.

Fig. 6. Eight-cell stage, side view; one polar body at animal pole.

Plate II.

Fig. 7. Eight-cell stage, apical view; each cell indented at periphery; polar furrows at right angles to each other at opposite poles.

Fig. 8. Seven-cell stage; irregular cleavage; animal pole indicated by three polar bodies.

Fig. 9. Sixteen-cell-stage, apical view; two polar bodies at animal pole.

Fig. 10. Sixteen-cell stage, optical section, showing blastocœl, ectoplasmic layer (*Em*) and polar body or yolk spherule between two of the cells.

Fig. 11. Twenty-cell stage; some of the cells elongated and probably dividing yolk spherules within blastocœl.

Fig. 12. About forty-eight-cell stage; egg flattened by pressure and the blastomeres partially separated.

Plate III.

Fig. 13. Early invagination stage, optical section.

Fig. 14. Gastrulation completed; blastocœl obliterated; gastrocœl partially divided into enteron (*E*) and enterocœl (*Ce*).

Fig. 15. Optical section of older embryo, viewed from posterior; enteron still further constricted from enterocœl.

Fig. 16. Optical section of embryo of same stage as preceding, lateral view, showing anterior extension of enterocœl and partition wall growing down on anterior side between enteron and enterocœl.

Fig. 17. Oral view of embryo, showing elongated blastopore opening at its anterior end into the enterocœl and enteron; the enterocœl but little larger than the enteron.

Fig. 18. Antero-ventral view of an embryo of about the same stage as the preceding.

Plate IV.

Fig. 19. Optical section of older embryo, viewed from posterior; showing the enteron separated from the enterocœl.

Fig. 20. Optical section of an embryo of same stage as preceding, lateral view; showing the enteron almost entirely separated from the enterocœl.

Fig. 21. Oral view of an embryo of about the same stage as the preceding; the blastopore narrower than in preceding stages; the enteron completely cut off from the enterocœl except in the region of the blastopore; mesenchyme cells (*mc*) line the anterior part of the enterocœl.

Fig. 22. Oral view of an older embryo in which the blastopore has closed to a narrow groove except for a small opening near its anterior end; mesenchyme cells are abundant in the anterior and posterior parts of the enterocœl; mantle folds show at the sides of the embryo.

Fig. 23. Aboral view of an embryo of the same stage as the preceding, showing dorsal mantle fold (*M*).

Fig. 24. Optical longitudinal section of an embryo in which the blastopore has completely closed, leaving however on the ventral surface the blastopore remnant (*Br*) and groove; the dorsal mantle fold (*Md*) and furrow are shown on the dorsal side; the enteron still communicates with the enterocœl at its posterior end.

Plate V.

Fig. 25. Dorsal view of a larva in which cephalic, mantle and peduncular regions are well defined.

Fig. 26. Ventral view of an older larva, showing the ventral mantle folds meeting in the region of the blastopore groove (*Bf*); the blastopore remnant (*Br*) lies in a notch on the anterior side of the mantle fold.

Fig. 27. Dorsal view of a slightly older larva, showing the increased prominence of the mantle and the lobulation of the cœlom.

Fig. 28. Optical longitudinal section of a larva of the same stage as the preceding, showing the dorsal and ventral mantle folds (*Md* and *Mv*); apical sense plate and ganglion; enteron and cœlom.

Fig. 29. Ventral view of an older larva, showing the ventral mantle folds fused in the midline; the anterior and posterior mantle furrows are shown as shaded lines; in the anterior mantle furrow the place at which the blastopore remnant disappeared and where the œsophageal invagination will occur is marked (*O*); the apical and ventral sense plates (*CG* and *SG*).

Fig. 30. Dorsal view of a larva of the same stage as the preceding, showing the dorsal mantle fold (*Md*); the anterior and posterior mantle furrows; the union between the two halves of the peduncular cœlom.

Plate VI.

Fig. 31. Lateral view of a larva of the same stage as the preceding, showing anterior and posterior mantle folds (*Fa* and *Fp*), apical and ventral sense plates (*CG* and *SG*), enteron and cœlom.

Fig. 32. Dorsal view of older larva, showing increased prominence of mantle and deep constriction of anterior mantle furrow.

Fig. 33. Dorsal view of an older larva, showing the mantle in process of growing back over the peduncle; the cœlom is almost entirely confined to the mantle.

Fig. 34. Dorsal view of one of the oldest free-swimming larvæ; the mantle has almost entirely covered the peduncle.

Fig. 35. Lateral view of a larva of the same stage as the preceding, showing apical and ventral sense plates (*CG* and *SG*), dorso-ventral extension of enteron and greater width of mantle chamber on dorsal side.

Fig. 36. Optical section in longitudinal frontal plane of a larva of the same stage as the preceding, showing apical sense plate and cerebral ganglion; mantle chamber and setæ sacs; cephalic, peduncular and mantle cœlom (*Cc*, *Cp*, *Cm*).

Plate VII.

Fig. 37. Section of an embryo of the stage shown in Fig. 13, showing dark staining granules in the outer ends of the cells and yolk spherules in the blastocœl.

Fig. 38. Section of an embryo of the stage shown in Fig. 14.

Figs. 39–42. Four transverse sections of an embryo of the stage shown in Fig. 20; Fig. 39 being the most posterior and Fig. 42 the most anterior section drawn.

Figs. 42*a* and 42*b*. Longitudinal sections through an embryo of about the same stage as is shown in Figs. 39–42, showing the formation of the septum which separates the enteron from the enterocœl.

Plate VIII.

Figs. 43–47. Five transverse sections of a larva of the stage shown in Fig. 24; Fig. 43 being the most anterior and Fig. 47 the most posterior section drawn.

Figs. 48–52. Five transverse sections of a larva of the stage shown in Fig. 29; Fig. 48 being the most anterior and Fig. 52 the most posterior section drawn.

PLATE IX.

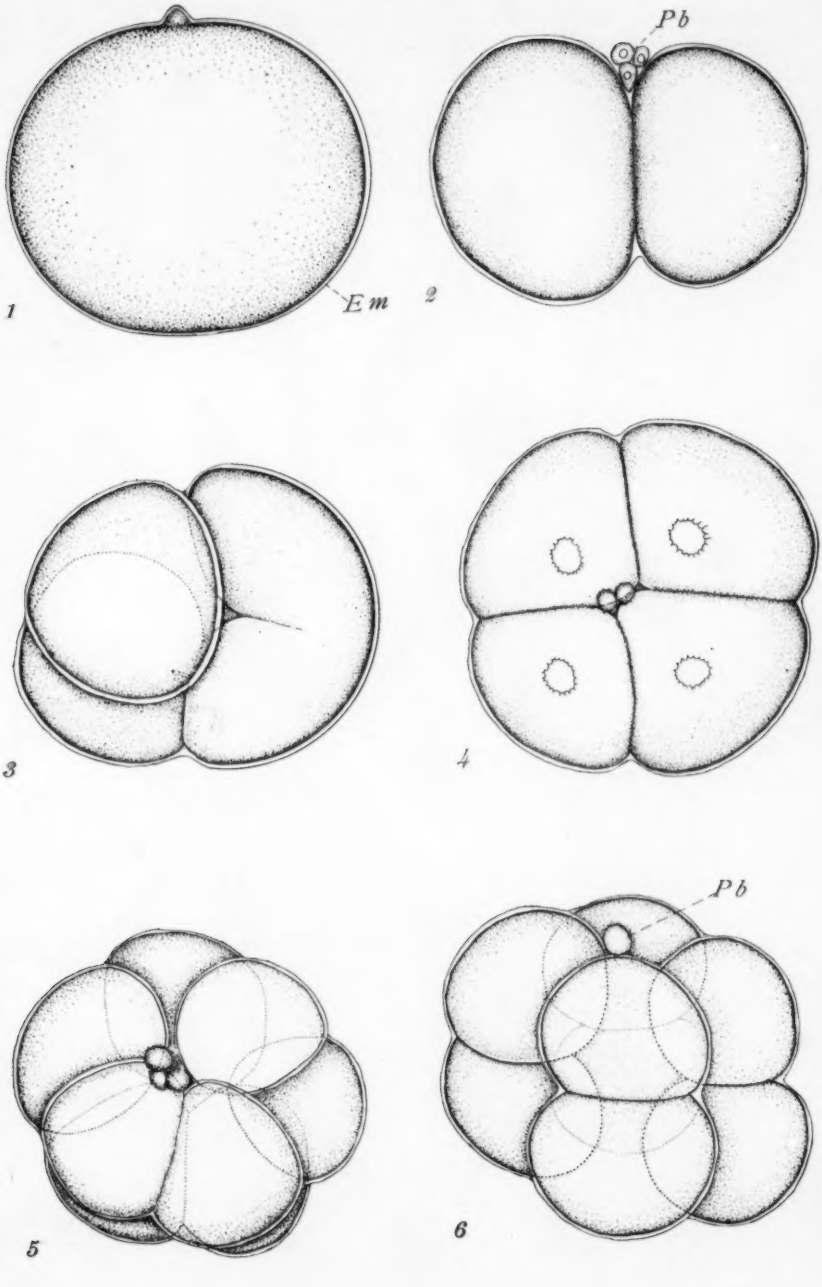
Figs. 53–55. Three oblique sections from the dorsal anterior (*DA*) to the ventral posterior (*VP*) region of a larva of the stage shown in Fig. 31 (the sections are nearly in the plane of the reference line from *E* in Fig. 31).

Figs. 56, 57. Two longitudinal frontal sections of a larva of the same stage as the preceding, Fig. 56 being ventral to Fig. 57.

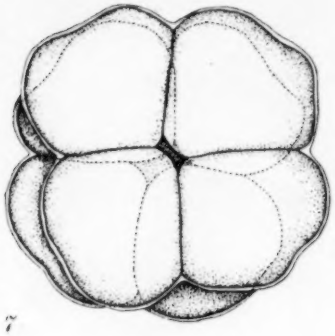
Fig. 58. Longitudinal sagittal section of a larva of the same stage as the preceding; the section passes through both the apical and the ventral sense plates (*CG* and *SG*).

PLATE X.

Figs. 59–64. Six transverse sections of a larva of the stage shown in Figs. 34–36; Fig. 59 being the most anterior and Fig. 64 the most posterior section drawn. Fig. 59 passes through the cephalic region; Fig. 60 lies just behind the anterior mantle furrow; Figs. 61–64 are through the mantle and peduncle.



CONKLIN ON TEREBRATULINA SEPTENTRIONALIS.



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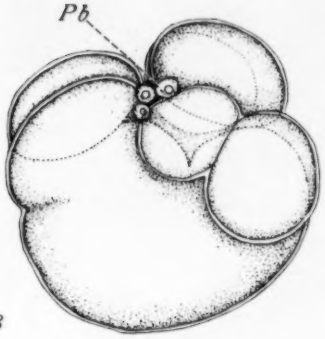

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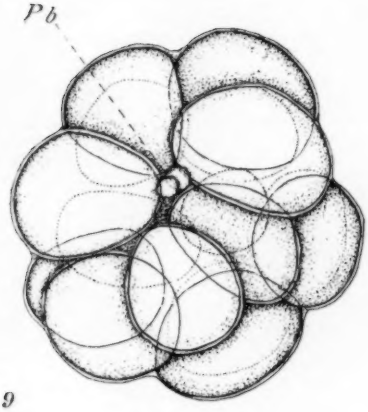

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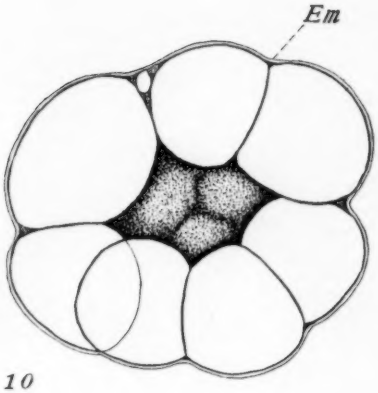

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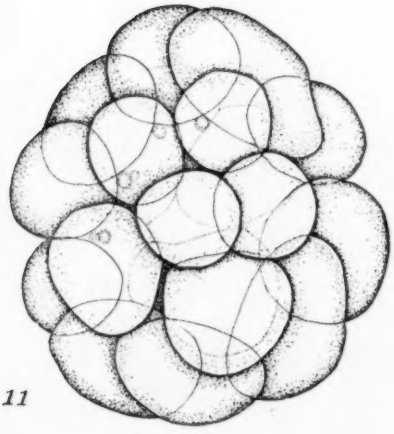

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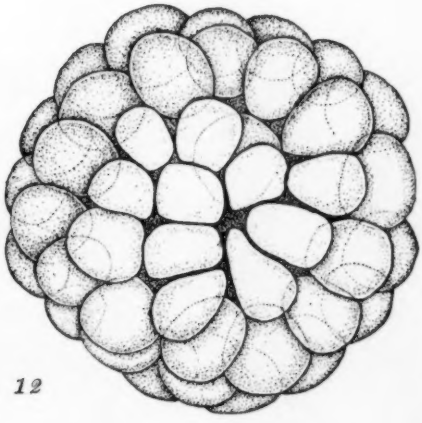

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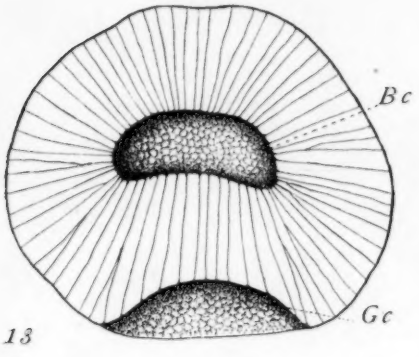

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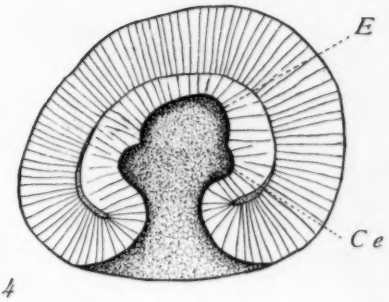

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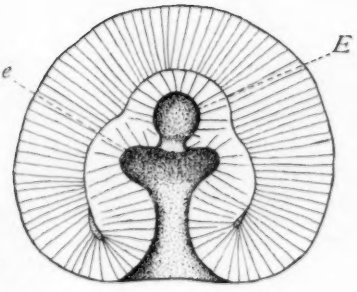

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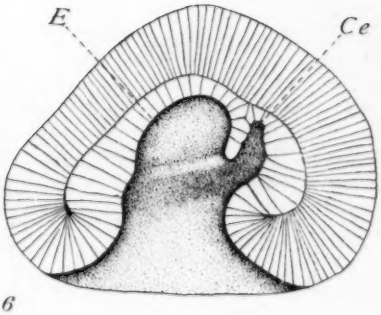

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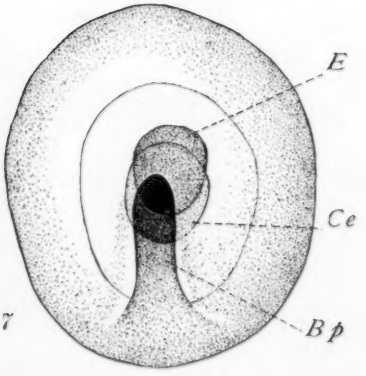

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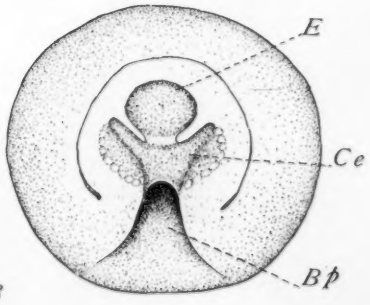

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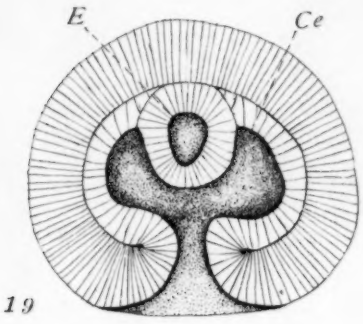

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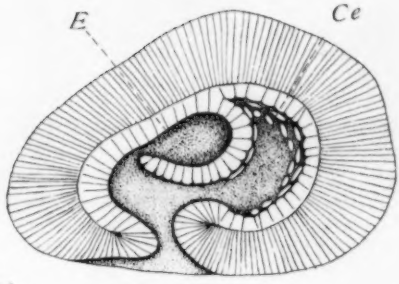

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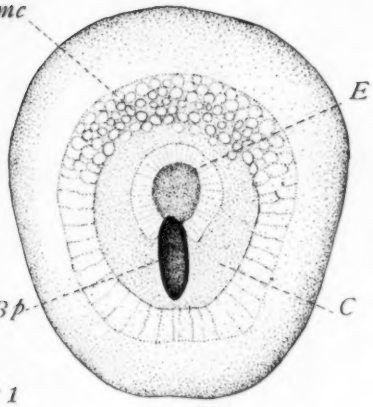

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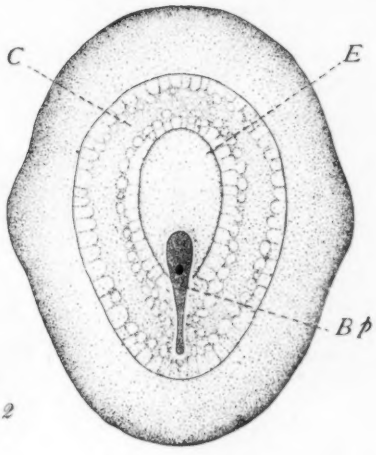

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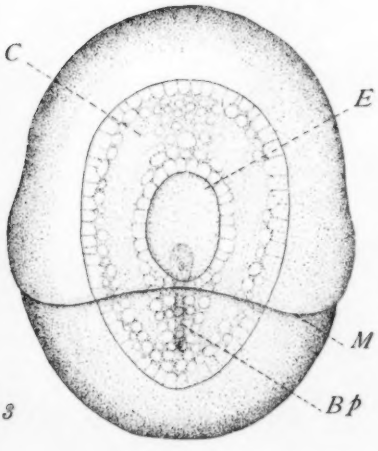

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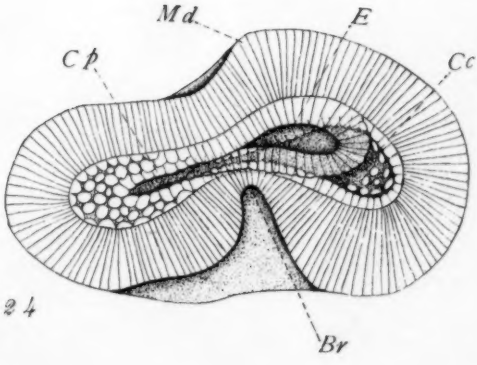

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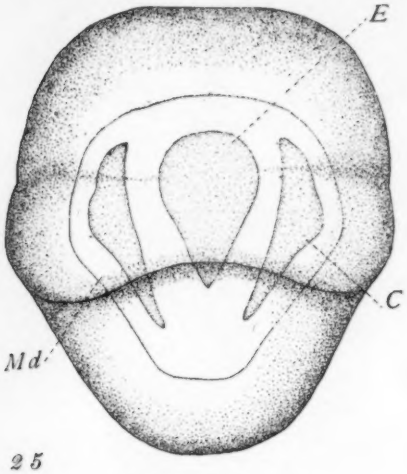

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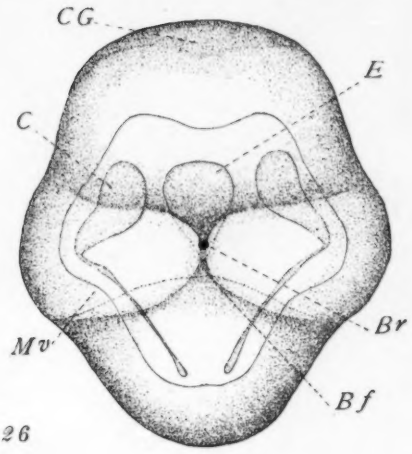

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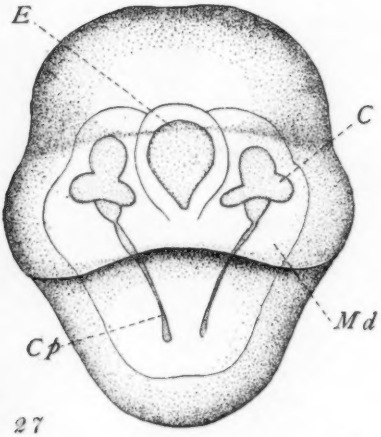

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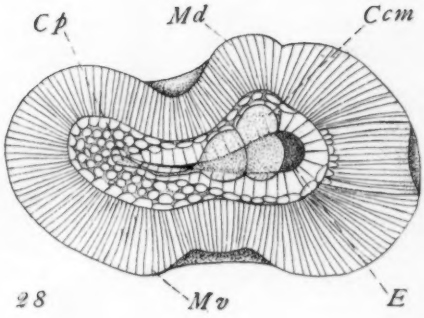

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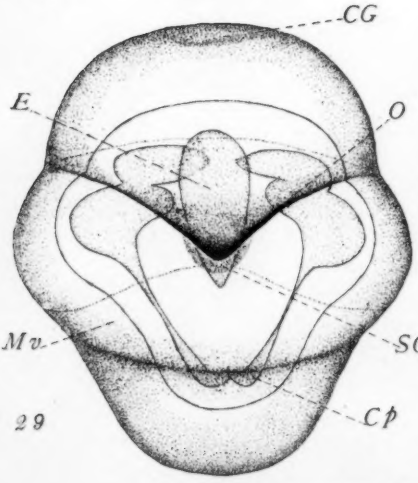

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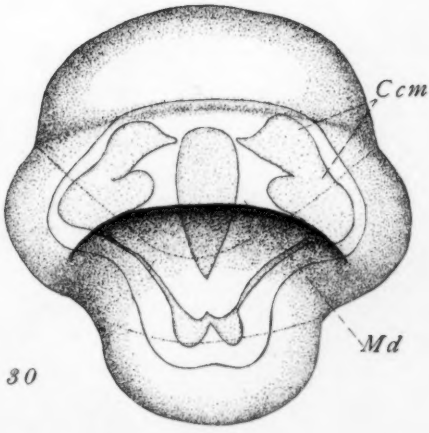

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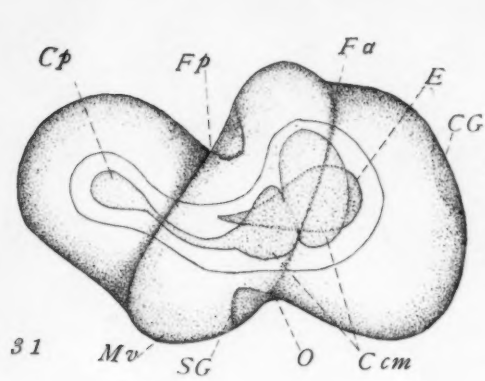

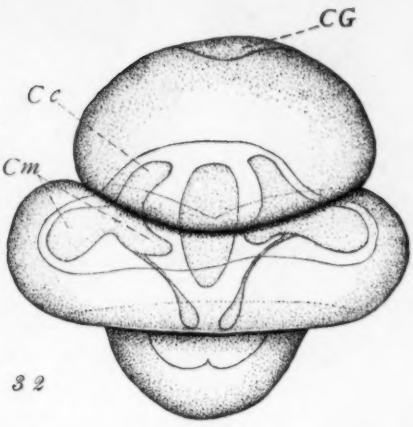

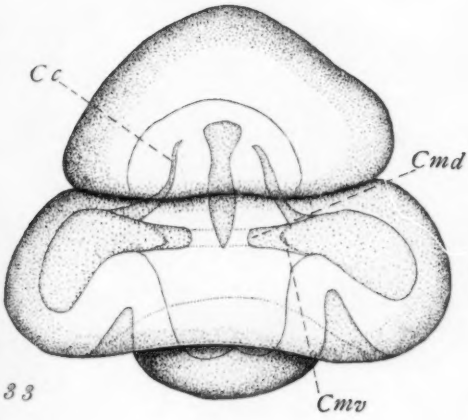

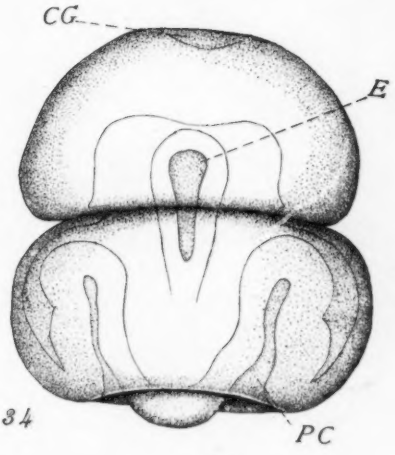

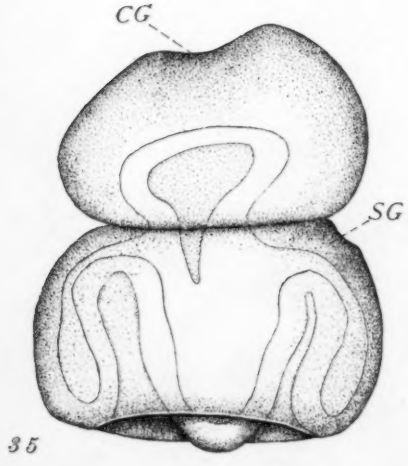

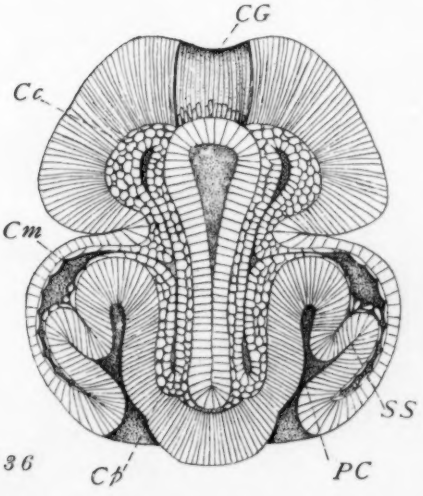

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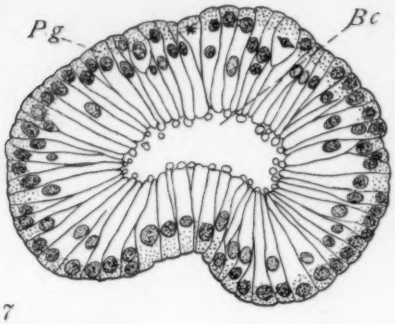

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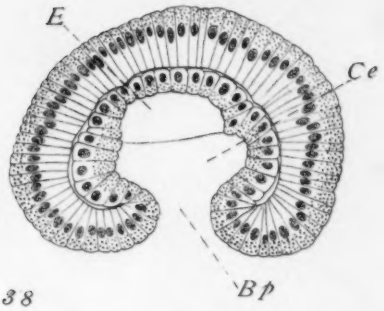

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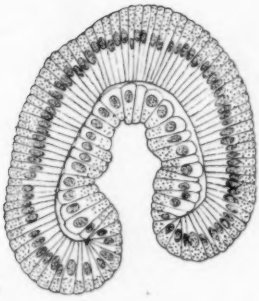

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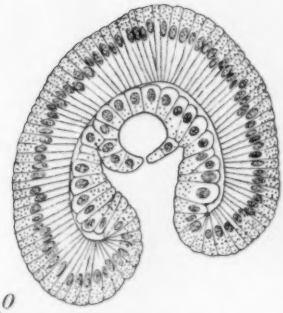

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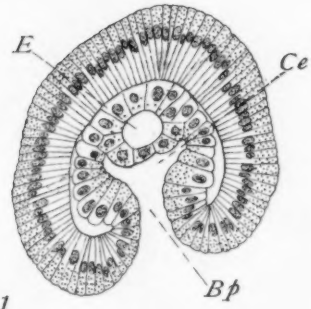

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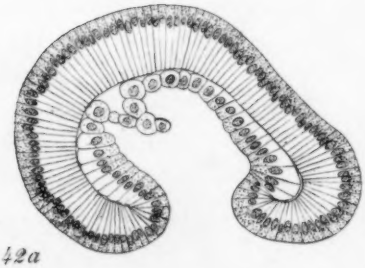

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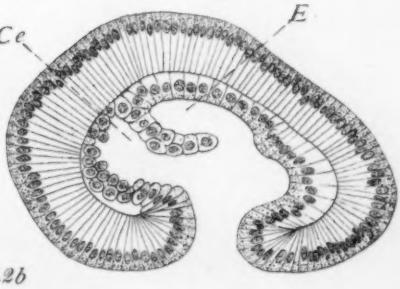

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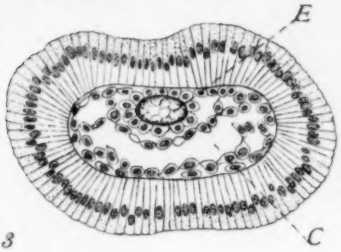

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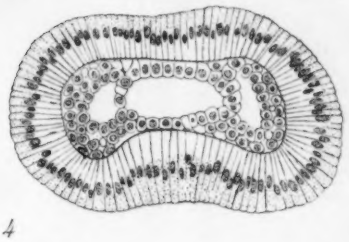
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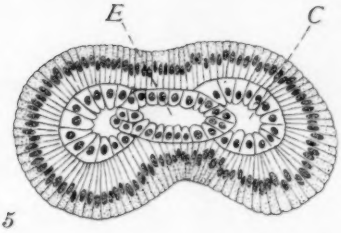

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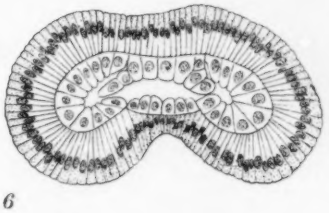
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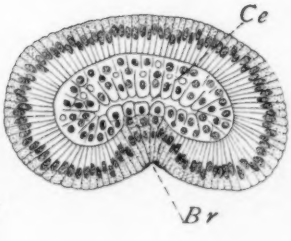

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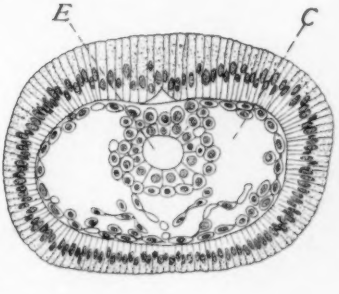

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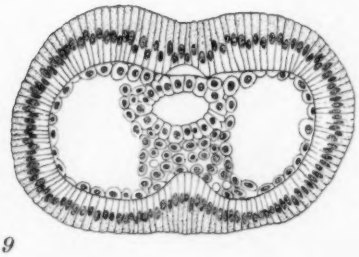
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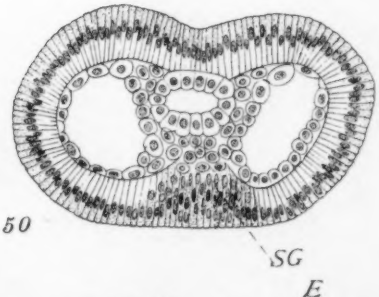

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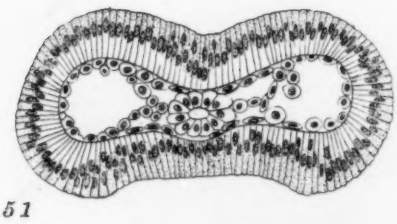
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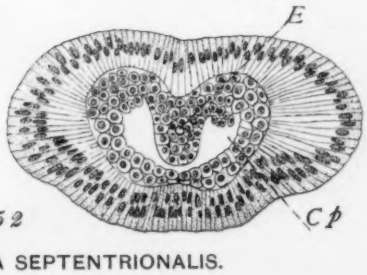

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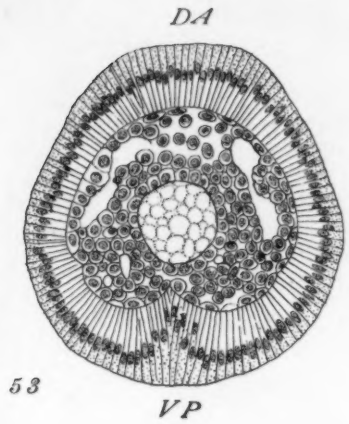
CONKLIN ON TEREBRATULINA SEPTENTRIONALIS.



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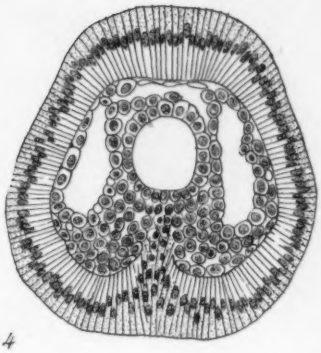
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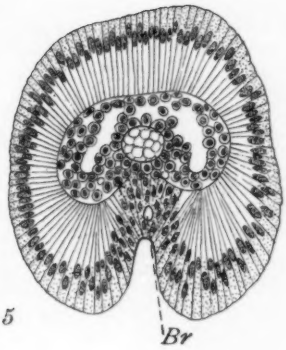

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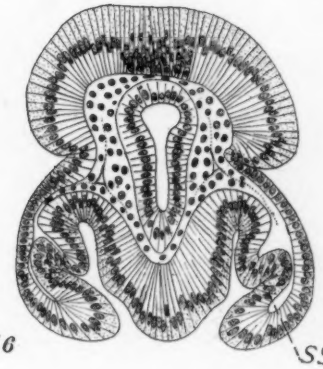

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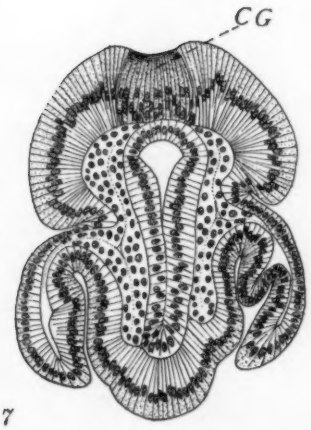

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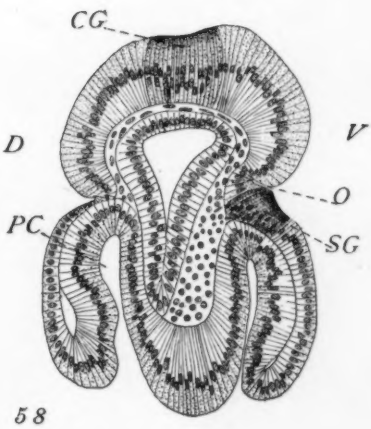

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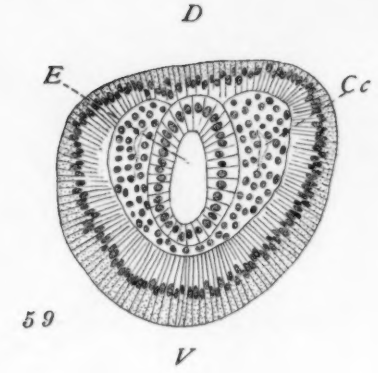
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59
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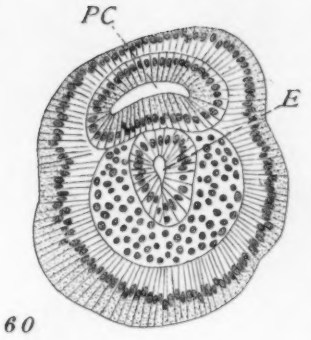
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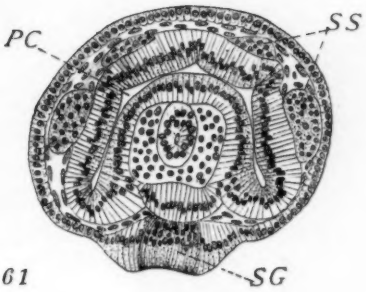
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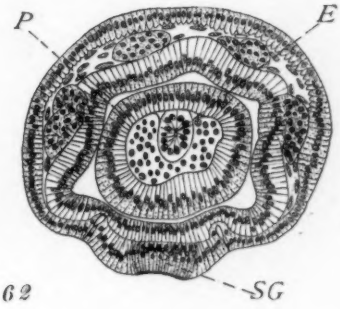
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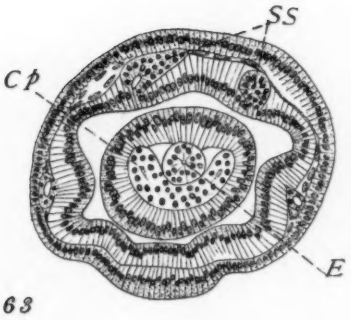
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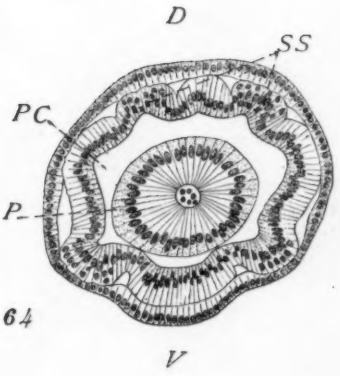
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THE SPERMATOGENESIS OF ONISCUS ASELLUS LINN.[1] WITH ESPECIAL REFERENCE TO THE HISTORY OF THE CHROMATIN.[2]

BY M. LOUISE NICHOLS.

(Plates XI-XVIII.)

(*Read April 4, 1902.*)

This study was begun in the month of February, 1899, in order to ascertain the mode of origin of the peculiar spermatozoa of the land Isopods. I have now completed, so far as I am able at the present time, the investigation undertaken for that purpose. Before entering, however, upon a description of my observations, I wish, at the close of a work which has proved both interesting and instructive, to express my gratitude to my instructors, Prof. E. G. Conklin and Prof. Thomas H. Montgomery, Jr., for the inspiration and the many valuable suggestions which have aided me toward its completion. To the latter I am particularly indebted for his helpful criticism concerning the earlier stages of the spermatogenesis.

METHODS.

The material was fixed either in Flemming's fluid, Hermann's fluid or in Gilson's fluid (acetic-nitric sublimate). It was stained for the most part with iron hæmatoxylin, but for purposes of comparison also with saffranin and malachite green (Wilcox) (1895), saffranin and gentian violet, Delafield's hæmatoxylin and Bordeaux red, and with the Biondi-Ehrlich triple stain. The study of the spermatozoa was also pursued by teasing apart the vas deferens with needles, staining the fresh material with hæmatoxylin or with acetic-methyl green, and mounting in glycerin. Permanent mounts were also made of fixed and stained material. I consider Wilcox's double stain with saffranin and malachite green to be a valuable one, for the reason that it can be used with good effect on material fixed in Flemming's fluid. It gives in reality a triple stain, for in successful preparations the cytoplasmic structures stain green, active chromatin, centrosomes and true nucleoli red, while resting chromatin takes a purple color. Its chief disadvantage is that it will in time fade.

[1] The species was determined by means of the works of Budde-Lund (1885) and of Richardson (1900). The species is also known as O. murarius, Cuv.

[2] A thesis for the degree of Ph.D. at the University of Pennsylvania.

I. Structure of the Male Reproductive Organs.

The male reproductive organs of the land Isopods are paired and lie on either side of the tubular intestine, occupying almost the entire length of the thoracic region.

The testis consists of three narrow lobes, which are attached to the body musculature by slight strands of tissue. These lobes are distinct from each other and open successively into the anterior expanded portion of the vas deferens (Fig. 1). Posteriorly the vas deferens narrows to a more slender tube, which joins its fellow of the opposite side and opens through the penis, which is unpaired and is said by Gerstaecker (1882) to be an outgrowth from the seventh thoracic segment. It is enclosed by the modified internal lamellæ of the first abdominal appendages (Fig. 1).

Sections of the vas deferens (Fig. 3) show its expanded portion to be lined with cells of large size, which possess prominent spherical nuclei. The nucleus is sometimes surrounded by a clear space, varying somewhat in size. The chromatin is in the form of closely crowded granules. Between these are sometimes other granules, which with the iron hæmatoxylin stain are less deeply colored, and with Bordeaux red and Delafield's hæmatoxylin take a red tint. The periphery of the latter is usually darker in color. The surrounding cytoplasm is filled with particles of a rounded shape, which take cytoplasmic stains (Fig. 4*a*). In one preparation the cytoplasm of these cells was filled with particles, not rounded in shape but thread-like, and taking a very dark stain with iron hæmatoxylin. The chromatin consisted of granules of varying size, which appeared lighter in the centre and possessed a darker margin (Fig. 4*b*). I do not know whether there is any connection between the particles within the nucleus and those without; the subject might possibly repay further research. The appearance of these cells suggests strongly that they have a secretory function; no doubt the fluid which bathes the spermatozoa is produced by them. They are more abundant at those places where the follicles open into the vas deferens and grow more scarce in the region where the narrow portion of the vas commences (Fig. 3). Between them are to be seen nuclei of smaller size, whose chromatin is not so distinctly and regularly granular. These lie in a cytoplasmic reticulum of a coarse mesh, without well-defined cell boundaries and containing no granules. This tissue apparently forms a supporting

membrane for the secretory cells. It is continuous with the layer of cells which line the narrow portion of the vas deferens and is similar to it in structure (Fig. 3). The narrow portion of the vas, as a rule, is covered externally by dark pigment, thus forming a marked contrast in the fresh state to the milk-white walls of the anterior portion (Fig. 1). Between the pigment layer and the lining cells, delicate muscle-fibres are occasionally discernible.

The three lobes of the testis are seen in section to be three follicles (Fig. 2). Each follicle is covered by a thin membrane which is provided with delicate muscle-fibres (Fig. 5*m*, *l*). The margins of the follicle are occupied by large nuclei of unsymmetrical outline, containing irregular blocks of chromatin interspersed with finer granules. Cell boundaries between these nuclei are not visible. They can sometimes be seen to be undergoing amitotic division, of a character similar to that described by vom Rath (1891) for Astacus (Fig. 5*f*, *c*). In follicles of a certain stage of development these nuclei, as will be explained later, are subject to degeneration.

The strands of tissue, by means of which the follicles are suspended from the body wall, are made up of cells which also divide amitotically and which are similiar in appearance to the follicle nuclei, inasmuch as their outlines are irregular, but the blocks of chromatin are of larger size and the nuclei are separated from each other by distinct cell walls (Fig. 6).

The interior of the follicle, except during the migration of the follicle cells, is occupied entirely by the germ cells, which are in differing stages of development in the three follicles of one side. Corresponding follicles of opposite sides of the body contain, however, germ cells which have developed to very nearly the same degree.

Fig. 2 shows, in a typical case, the comparative degrees of development to which the cells of the three follicles have attained. Each follicle may be divided into two principal regions of growth, composed of cells of different generations and of different degrees of development. Thus, in the most posterior of the follicles (*a*), the apical third is occupied exclusively by spermatogonia, some of which can be seen in mitosis; the basal region, on the other hand, by spermatids in a not very advanced stage. Follicle cells occur on the outside of the follicle, being especially abundant in the basal region. In the adjacent follicle (*b*), the apical two-thirds is occupied by cells in the synapsis stage, the remaining portion by sper-

matids in a stage of development later than that of follicle (*a*). Along the margin of the follicle are found scattered small groups of spermatagonia (Fig. 2, *spg*). The third and most anterior follicle (*c*) contains chiefly spermatocytes in a late prophase. Groups of spermatogonia similiar to those of follicle (*b*) are here also found scattered along the margin and nearly filling the extreme apical portion. The follicle cells in the basal region are undergoing not only active amitotic division, but to a certain extent degeneration (Fig. 5). Their active multiplication or fragmentation causes them to crowd in toward the axis of the follicle.

From a comparison of the extent of these growth regions in the three follicles, the developmental cycle may be conceived somewhat as follows. The spermatozoa, when fully formed, are forced into the vas deferens. Since they have no motion of their own, this is probably caused by the contraction of the muscle layer of the follicle, perhaps assisted by the pressure of the growing cells in the apical region. During this process, the spermatogonia in the apical portion of the follicle divide and come to fill the space left vacant by the discharged sperm. The rate at which this replacement takes place and the comparative development of the cells in the two regions may vary in different follicles, for I have preparations in which few or no spermatozoa are seen—in other words, most of them had probably been discharged, and at the same time the replacing spermatogonia are scattered and few in number. In others, as is shown in the diagram (Fig. 2*a*), the spermatozoa, in an early stage of development, occupy the basal portion of the follicle, while the apical portion is packed with spermatogonia. The majority of the spermatogonia thus filling up the follicle proceed in their development, while the remainder form the groups of cells along the margin of the follicle already described in follicles (*b*) and (*c*), and which are destined later to again supply a new generation of cells. The spermatids also proceed in development and are forced into the vas deferens. A condition like that represented in diagram (*b*) (Fig. 2) thus arises—the basal region filled with spermatozoa in a late stage about to pass into the vas deferens and the apical region with cells which have progressed as far as the synapsis stage. Later, the spermatozoa having been completely discharged, the cells of the apical region come to occupy the basal part of the follicle, being now less compactly pressed together (Fig. 2*c*). Their development progresses until, having become mature spermatozoa, they pass into

the vas deferens, the spermatogonia again fill the apical region, and the cycle is repeated.

The invasion of the follicle cells begins, as a rule, when the germ cells are in an advanced prophase and may continue later. Many of the germ cells likewise degenerate, and they, together with the follicle cells, form a disintegrated mass in which the spermatids lie. In young follicles, which have not as yet matured sperm, the basal region is filled with follicle cells, the apical region with spermatogonia. This is sometimes true also of older follicles which have recently discharged the sperm.

It will thus be seen that a series of stages, illustrating the complete history of the changes through which the germ cell pass, can be obtained only by an examination of numerous testes. Duplicates are often obtained and some of the stages occur very infrequently, probably owing to a greater rapidity of development at certain periods.

This study was begun in the latter part of February. In March or April, according to the rigor of the weather, the land Isopods in the vicinity of Philadelphia commence to breed. The breeding season continues during the summer months. There are, in a single year, several cycles of development of the reproductive elements; the exact number I have not determined. It is therefore possible, at almost any time of year, by examination of a sufficient number of individuals, to procure a complete series of developmental stages.

II. Spermatogenesis.

1. Spermatogonia.

The resting spermatogonia are distinguished from the follicle cells by their smaller size, the distinctness of the cell walls, and by the fact that in their nuclei the chromatin masses are of smaller size and show indications of an arrangement into a network (Fig. 11*a*). They possess a prominent true nucleolus of more or less rounded form. Some cells contain one or more smaller nucleoli.

It is impossible to determine the exact number of spermatogonic divisions. They are probably numerous, since it must require a considerable number of divisions of the spermatogonia remaining in the follicles to fill the space left vacant by the discharged sperm. The cells vary somewhat in size. When the apical region of the follicle is filled with spermatogonia the individual cells are small, but when the follicle is not well filled and the spermatogonia are

beginning the task of producing a new generation, individual cells often equal the spermatocytes in size (Figs. 10 and 13). In the cytoplasm are occasionally seen irregular masses of a dull brown tint (yolk?), but neither sphere substance nor centrosomes are apparent in the resting cell.

In nuclei preparing to divide, the chromatin is seen to be arranged in the form of slender, elongated threads, which, so far as I have been able to discover, in no case form a continuous spireme (Fig. 7). In the cytoplasm surrounding a nucleus of this character are visible two minute black specks joined by a delicate thread, presumably the centrosome undergoing division. The nuclear membrane at this stage begins to fade. Figs. 8, 9 and 10 show stages immediately succeeding the stage shown in Fig. 7. The threads have become shorter and thicker, the nuclear membrane has entirely disappeared, and the centrosomes have become more widely separated. The amount of segmentation of the thread varies in different cells. In Fig. 11*b* is shown a nucleus in which very little segmentation has taken place, although the thread is considerably thicker than that shown in Fig. 7. The linin threads joining the chromosomes are of extreme delicacy and difficult to discover. Occasionally, however, (Fig. 9) fine fibres may be seen stretching from one chromatin thread to the next. The shortened and thickened chromosomes then arrange themselves into an equatorial plate (Fig. 12). The appearance of the plate, both in side and in pole view, is irregular. The division of the chromosome into chromomeres and their longitudinal division is visible only in very thin sections, which have been stained with iron hæmatoxylin and rather strongly decolorized (Fig. 14). The centrosomes and spindle-fibres of the spermatogonic, mitotic figure are not quite so prominent as those of the spermatocytic divisions. The same is true of the polar radiations. Central spindle-fibres are apparently entirely lacking. After splitting of the chromosomes the halves diverge, in the manner of the two legs of a pair of compasses, the divergence commencing at one end, while at the other end the two halves remain in contact (Fig. 15).

A still later anaphase is shown in Fig. 17. The chromosomes have become massed together, the spindle-fibres are beginning to disappear and the centrosomes are almost lost to sight. The constriction of the cell body, observable to a slight degree at this stage, becomes more marked and a membrane comes to separate the two daughter cells (Fig. 19).

The reconstruction of the nucleus consists of the breaking up of the chromosomes into fine granules, which are connected by linin threads of great delicacy, and in the development of a nuclear membrane (Figs. 19, 20, 21). The change in chemical composition of the chromatin is indicated in sections stained with saffranin and gentian violet by a gradual change in color from red to blue. As the cell body constricts slight thickenings are discoverable on the connective spindle-fibres in the equator (Fig. 18), which, as the constriction proceeds, grow fewer in number and more conspicuous in size until they are finally reduced to a single large swelling, from which radiate the spindle-fibres, by this time grown faint (Fig. 19). At a stage a little later than the one just described I have occasionally seen a small black body wedged in the angle between the daughter cells (Fig. 20). Its appearance is similar to the "Flemmingscher Körper" described by Hoffmann (1898) for *Limax maximus* (see his Figs. 31, 32, 33) and strikingly like that of the rabbit described by von Winiwarter (1900, Figs. 9 and 10).

2. Growth Period.

The anaphase of the last spermatogonic division is decidedly different from that just described. The chromatin threads lie massed together and entangled near the centre of the cell (synapsis). They are surrounded by a clear space bridged over by slender acromatic fibres, which connect the chromatin threads with a narrow layer of cytoplasm lying close to the cell wall. No trace of centrosome or sphere substance (idiozome) is discoverable (Fig. 22). The chromosomes now spread apart, although still connected by strands of linin. They are seen to be for the most part V-shaped. The chromatin granules are rather irregularly distributed, being frequently massed together in lumps (Fig. 24).

In a thin section of a cell at a stage slightly later than this there appeared a minute black dot, surrounded by a vaguely defined area, slightly more dense than the rest of the cytoplasm (Fig. 23). I hesitate to attach importance to this, as it occurred in very few cases.

The threads now elongate, and during this process the granules of which they are made up divide, so that the thread becomes longitudinally split. The granules apparently do not divide simultaneously. Even in the same thread some of them show division, while others remain entire (Fig. 25). The split is to be seen with

the greatest clearness in sections stained with iron hæmatoxylin and strongly decolorized. The chromosomes are very irregularly distributed, only occasionally a part of them, six or seven, may be grouped with reference to a central point. Of the entire number of chromosomes present it is difficult to be certain, owing to the fact that they overlie each other so closely. The number, however, is certainly less than that present in the spermatogonia and not greater than sixteen (Fig. 26). The reduction in the number of chromosomes, therefore, apparently takes place at this stage, and the V-shape so prevalent is due to the approximation of two chromosomes to form a single bivalent one. The place of union is frequently covered by chromatin, but a connection of linin can sometimes be discovered (Fig. 27). This figure also shows the varying angle at which the univalent chromosomes may approach each other. Occasionally they may even form a complete ring.

The threads become more and more attenuated (Fig. 28), and finally by anastomosis are transferred into the nuclear reticulum of the resting spermatocyte (Fig. 30). During the elongation of the chromosomes the chromatin granules divide and redivide (Figs. 23–28), so that they become very numerous, and as the elongation progresses the longitudinal split becomes less easily discoverable, until in the resting cell it can no longer be made out. Cells are sometimes seen in which, just before the formation of the nuclear membrane, the network lies to one side, being connected by slight strands of linin with the surrounding cytoplasm (Fig. 31).

The fact that the chromosomes remain distinct until just before the formation of the nuclear membrane points to a maintenance of their individuality in the resting cell.

The nuclear membrane appears to form as a condensation of achromatic substance, upon which later appear granules staining deep blue with hæmatoxylin (Fig. 29).

A peculiar fact with reference to the last spermatogonic division has struck my attention and I have been unable to explain it very satisfactorily. It will be seen from Fig. 2 that nearly all the cells in the apical portion of follicle (*b*) are in the synapsis stage. It might be supposed from this that sections would be obtained of follicles filled apically with the spindles of the last spermatogonic division. Such a condition, however, I have never found, although I have examined a large number of testes at different seasons of the

year. The karyokinetic figures of the spermatogonia are always scattered and it is impossible to distinguish between the early and late ones.

3. The Maturation Divisions.

In preparing for the first maturation division the meshes of the nuclear network become coarser, the granules more distinct and aggregated into separate threads, joined together by linin (Figs. 32–36). The manner of their origin again lends support to the view concerning their individuality in the resting cell. A still greater condensation of the granules leads to a shortening and thickening of the chromosomes (Figs. 37 and 38), the final result of which is the production of sixteen compact masses of chromatin, still connected by linin threads (Fig. 44). Condensation does not proceed at an equal rate in all the chromosomes of a nucleus. Fig. 45*a* shows a small portion of a nucleus in which lie side by side two chromosomes, in one of which the final dumbbell-shape is almost completed, while in the other the condensation of the chromatin is but little advanced. These sixteen masses are of various forms. Some are dumbbell-shaped, two spheres of chromatin joined by linin; some are crescent-shaped and still others are more or less complete rings (Figs. 39–45). The different forms may occur in the same nucleus, but apparently without constancy in the ratio of relative frequency of occurrence. The dumbbell-shape, straight or slightly curved, is abundant, some cells containing no complete rings (Fig. 41). Other cells contain a comparatively large number of rings or crescents (Figs. 39 and 40).

Two main types may be distinguished among the chromosomes according to their structure and mode of origin—*i.e.*, (1) those in which the bivalent chromosome consists of two univalent chromosomes lying end to end, as in those having the dumbbell-shape, and (2) those in which the univalent chromosomes lie side by side, as in those arising through a ring or narrow V-shape. A form intermediate between these is represented by those having a crescent-shape. The different types and their probable mode of origin are shown in the diagram (Fig. 68*a*, *b*, *c*). It is interesting to note that these types can be distinguished in the synapsis stage (Fig. 27), although they are here not so well marked as in the prophases of the first maturation division.

In cells stained with iron hæmatoxylin, which have been strongly

decolorized, a longitudinal split is evident and likewise a division of the chromosome into chromomeres. If the chromosome is of the second type and seen from above, two of the chromomeres will be seen longitudinally split (Fig. 46; *cf.* Fig. 53). An end view of a chromosome of the first type shows simply a single chromomere longitudinally split (Fig. 59).

Linin connections between the chromosomes are much more evident than in the spermatogonia, and they can be seen to extend from the sides as well as the ends of the chromosomes.

With regard to the origin of the first maturation spindle-fibres it is difficult to be certain, but they appear to arise, at least in part, from within the nucleus. The centrosome is not evident until a rather late prophase (Figs. 39, 40, 43). In many cases it lies within a more densely staining mass of cytoplasm of ill-defined outline applied close to the nucleus (sphere substance, idiozome of Meves) (1898) (Figs. 39*a*, 43). This is not, however, invariably the case, as may be seen from Figs. 40, 39*b*, where the centrosomes lie freely in the cytoplasm. Fig. 38*b* perhaps represents an early stage in the development of the sphere substance. In the two adjacent cells (Fig. 38*a* and 38*c*) are shown rounded bodies of a dull tint lying within clear vacuoles. I met these in but one preparation and am unable satisfactorily to interpret them. The division of the centrosome and the formation of the spindle is shown in Figs. 46, 47, 48, 52. The centrosomes and spindle-fibres, as well as the polar radiations, are more prominent than in the spermatogonic spindles. During this time the sphere substance disappears.

In the equatorial plate the chromosomes become arranged with the longitudinal split parallel to the axis of the spindle in the case of chromosomes of the first type, but at right angles to it or nearly so in the case of chromosomes of the second type (Figs. 49, 50 and 53). In Figs. 55 and 56 are represented pole views of both types of chromosomes. It may be gathered from these, as well as from the figures of the prophases, that chromosomes of the second type are not nearly so numerous as those of the first nor so numerous as those of the intermediate type.

From what has been said with regard to the origin of the chromosomes, it will be seen that in the metaphase the bivalent chromosomes are separated into their univalent components, and consequently the *first division is one of reduction.*

A well-marked mid-body is visible in the late anaphase (Fig. 61*a*). The interzonal fibres are sharply constricted and oftentimes the nuclei completely separated before a cell wall makes its appearance. In stages like this a noticeable bending of the fibres is often observed. This is slightly evident in Fig. 61*a*.

Apparently the plane of the second spermatocytic division is to be at right angles to the first, if Figs. 61*a* and 61*b* are interpreted as early stages in the formation of the equatorial plate of the second spermatocyte.

The equatorial plate of the second spermatocytic division is shown in lateral view in Fig. 62. The length of the chromosomes is less than that of the chromosomes of the first spermatocytic division. The question as to whether the second division is actually equational is difficult to decide. The chromosomes of the first maturation figure, consisting of a double row of four granules, are separated by karyokinesis into halves, and each half contains a double row of two granules (Fig. 58). It thus has the appearance, although only the appearance, of a true tetrad. It will be seen that some of these daughter chromosomes have a length equal to their width, whereas in others the length is slightly greater than the width. If we turn to the fully-formed spindle of the second division (Figs. 62, 63) we find similar phenomena. It might be argued from these appearances that the second division is also reducing. In view, however, of the weight of evidence in favor of both methods of division (equation and reduction) being necessary to the maturation of the sexual cells among the Arthropods, I hesitate to accept this interpretation without further corroborative evidence. When the length of the chromosomes is equal to their breadth, it is obviously as impossible to decide here concerning the plane of division as in the case of the true tetrads of the Copepods, *Canthocamptus*, *Heterocope* or *Diaptomus*. If the length is greater, as in the anaphase, the appearance might be referred to the elongation of the mother chromosome (Figs. 49, 51, 53), some of the daughter chromosomes not having recovered from the stretching apart of the chromatin in the metaphase. The apparently greater length of some of the chromosomes in the spindle of the second division (Fig. 63) may be explained by the assumption that some of the chromosomes commence to divide earlier than others, and consequently become elongated, an assumption which is not without parallel in the first spermatocytic and especially in the sperma-

togonic divisions (Fig. 15). In Fig. 61, a stage intermediate between 58 and 62, some of the chromosomes likewise appear of greater length than others. It might be supposed that the longer ones represent the side view, the shorter ones the end view, of the chromosomes. This need not, however, necessarily be the case, for the chromosomes vary amongst themselves in size (Fig. 58 and previous figures). It is possible, too, that in some cases the chromosomes are seen slightly foreshortened and that their true dimensions do not appear in the figure. I feel it, therefore, impossible to ascertain with the desired degree of certainty the plane of the second spermatocytic division.

In the late anaphase (Fig. 66) the chromosomes are more or less indistinguishably massed together. On each of the interzonal fibres in the equator is a minute swelling. These become reduced in number (Fig. 67).[1]

4. Metamorphosis of the Spermatids.

The chromosomes spread apart, a nuclear membrane is developed and the daughter cells become the spermatids. The gradual conversion of the chromosomes into a fine reticulum is illustrated in Figs. 69 and 70.

The nucleus now commences to elongate at one end (Fig. 72), and this continues until the entire nucleus is transformed into a shape somewhat like that of a narrow flask (Fig. 74). The nuclear network is extremely delicate and takes the iron hæmatoxylin stain more faintly than previously. In cross section (Fig. 74*b*) numerous fine dots appear interspersed with clear areas (vacuoles). This vacuolated appearance is sometimes evident at an earlier stage (Fig. 71).

During the transformation of the nuclei the cell boundaries have entirely disappeared and the nuclei lie in a common mass of cytoplasm. Several of them become associated together, and their extremities, elongated into slender threads, are surrounded by a clear, homogeneous, well-defined area of cytoplasm, while the more or less contorted bodies of the nuclei still lie in an undefined mass of cytoplasm (Fig. 77*a*).

A cytoplasmic thread of extreme delicacy can be traced from the

[1] During the examination of the foregoing stages I have seen nothing similar to the accessory chromosome (chromatin nucleolus) of insects, as described by Montgomery (1898) and Paulmier (1899).

slender extremity of each nucleus for some distance into the clear, homogeneous area (Fig. 77*a*). At this stage also there can be clearly seen in the undefined mass of cytoplasm a bundle of fibres, which run in between the nuclei, but which cannot be seen to have any connection with them. I have a preparation of a stage, earlier than that just described, stained with hæmatoxylin and Bordeaux red, in which these striations appear, near the margin of the follicle (Fig. 73). So early a development of the fibres is rather unusual. The fibres are here apparently incomplete and not massed together as they later are. On account of their indistinctness it is difficult to say whether or not they are independent of the nuclei. At first sight it might appear as if they were continuous, but it is impossible to state definitely that this is so because of the impracticability of tracing a single fibre for any great distance.

The further changes in the nuclei consist in their gradual elongation into filaments, in which the network has entirely disappeared and which have acquired the power to take a vivid and homogeneous stain. Their free ends, at first divergent, gradually approach each other and finally come to lie close together (Figs. 77–79, 85 and 86). In regions of the follicle where the cells are closely crowded together the nucleus is often seen to be bent or coiled upon itself (Fig. 83).

There is at first a small quantity of cytoplasm around the nuclei, but as they increase in length this disappears. The cytoplasmic fibres also increase in length at the expense of the surrounding cytoplasm. Their length, indeed, becomes truly marvelous, many times exceeding that of the nuclei. They crowd in between the follicle cells (Fig. 2) and in cross sections of the follicle can be seen in great numbers around the margin. From the anterior end of the bundle is developed a slender flagellum (Figs. 85, 86). The entire bundle has the appearance at first sight of a single spermatozoon, and such I thought it before having studied its development.

The term "spermatophore" has been applied by Gilson to the bundle. This term, however, has been used by Grobben and others to designate an envelope secreted by the cells of the vas deferens (in the Decapods) and surrounding a mass of spermatozoa. It does not, therefore, seem applicable to the bundle of spermatozoa found in the Oniscidæ. Ballowitz applies the term "spermozeugma" to a large bundle of double spermatozoa found in the vas deferens

of the Dytiscid, *Colymbetes striatus*. These adhere together after having reached maturity. Their structure and mode of origin is, therefore, not the same as that of the bundles of Oniscus. The term "compound spermatozoon" has been suggested to me, but the word spermatozoon might carry with it certain implications with regard to behavior in fertilization. I prefer, therefore, to use the term sperm colony, at least until a better one offers itself. Gilson uses this term also, although not so generally as the word "spermatophore."

The number of nuclei entering a colony varies within rather wide limits. I have counted as few as six and also as many as fourteen. In cross sections stained with saffranin and malachite green, they are seen as red bodies surrounding a central mass of green dots, the sections of the cytoplasmic fibrils (Fig. 80). The red dots diminish in size toward the anterior end of the bundle, and at one point can be seen merging directly into delicate green threads (Fig. 80*b*). At the extreme anterior end of the bundle the delicate green threads alone will be cut (Fig. 80*a*). It might be supposed that the bundle of cytoplasmic fibres previously described are the tails of the spermatozoa. If they are really the tails of the spermatozoa, one would expect to find them at some place connected with the nuclei, or with the delicate fibres which can be demonstrated to be continuous with the nuclei. A comparison of sections obtained at different levels seems to leave but two alternatives: either the long bundle of cytoplasmic fibres stops abruptly before the anterior end of the colony is reached, or the connection is of so tenuous a character as to escape observation. In structures of such minuteness the latter might easily be the case.

A point bearing on this matter, and therefore of interest to determine, is the number of cytoplasmic fibres as compared with the number of nuclei. Attempts to determine this might be made in two ways. The mature sperm colonies taken from the vas and teased apart might be examined and an attempt made to count the fibres at the frayed end of the bundle, or one might try to count the number as seen in cross sections. By either method it is difficult to be sure of an accurate count, for in the frayed ends of colonies one or more of the fibres may adhere together. In cross sections the fibres appear as minute dots, as a rule, closely crowded together. Occasionally they may be more loosely distributed. Fig. 81*b* represents a cell of this sort in which the number of cyto-

plasmic fibres equals that of the nuclei. I cannot be certain that this is invariably the case. With the iron hæmatoxylin stain the bundle of cytoplasmic fibres stains deeply, like the nucleus, and it is therefore impossible to distinguish between them in cross section where both appear. The delicate fibril previously mentioned, which joins the nucleus, stains faintly and can therefore be distinguished from the nucleus. In Figs. 81 and 82 cross sections of sperm colonies at slightly different stages of development, colored with this stain, are compared. In both images may be seen similar to that of Fig. 80—*i. e.*, a circle of dots merging into faintly staining fibres. Sometimes the latter have a granular or beaded structure (Fig. 81*a*). These are sections near the anterior end of the colony, and here again the central circle of dots, representing the posterior cytoplasmic fibres, is lacking. Fig. 82*b* represents a section which I interpret as having been cut slightly posterior to Fig. 82*a*. The tail fibres here begin to appear.

A comparison of the two stages illustrates the gradual dwindling of the cytoplasm which surrounds the bundle. It will be remembered that shortly after the complete reconstruction of the spermatid nucleus, cell boundaries disappear and the nuclei lie in a common plasma. When, however, the nuclei come to be associated in groups, the cytoplasm again becomes sharply defined and in cross sections an appearance like that of separate cells is obtained (Fig. 80). The cytoplasm in the anterior region becomes comparatively homogeneous and the nuclei often lie in a central clear space (Fig. 81*a*). More posteriorly it breaks up and assumes a granular appearance (Fig. 81*c*), while still farther back the fibrillar bundles lie isolated, with vague remnants of cytoplasm between them (Fig. 81). In Fig. 82 the diameter of the colony is less and the cytoplasm surrounding the fibres decidedly less extensive.

The sperm colonies when mature, or nearly so, are forced into the vas deferens, probably by contractions of the muscle layer of the follicle. In the vas they are surrounded by a fluid secreted by the large cells which form its lining, and which causes them readily to adhere to needles or forceps. The mature colony has the appearance shown in Figs. 85, 86 and 87. I have not heen able to isolate a single colony entire, for in teasing the long fibres are almost invariably torn. I have been able to trace them for a considerable distance, however, and can state that they are exceedingly long. The filamentous nuclei are invariably partially frayed from the

sheath and often entirely torn from it, lying twisted and contorted at some distance from the sheath. According to Hermann, 1883 (*2*), the spermatozoa of the Isopods retain their immobility in the oviduct of the female. The function of the extraordinarily long fibres, if the spermatozoa remain motionless, is to me a matter of great perplexity. It becomes still more puzzling if, as my preparations seem to indicate, there is no direct connection between them and the nuclei. Their function and their true relation to the nuclei might possibly be elucidated by a study of their behavior in fertilization, a study in which I hope to engage at some future time.

5. The Nucleolus.

In the resting spermatogonia the nucleolus is present as a rounded or oval body, staining pink with the eosin of the Biondi-Ehrlich stain and red with saffranin. When the mitotic figure is fully formed it is, as a rule, no longer visible, nor is it seen in the prophase immediately preceding. The newly constructed daughter nuclei likewise show no trace of it (Figs. 10, 14, 20). Possibly it may consist of metabolic products developed in the resting cell and quickly dissolving during or before mitosis. In the synapsis stage, subsequent to the last division of the spermatogonia, the nucleolus is, however, clearly visible, lying to one side of the tangled mass of chromatin threads.

In the very earliest synapsis of which I have sections it is not discernible (Fig. 22), but as the threads elongate and separate it becomes evident. It continues to be present throughout the synapsis and is finally enclosed within the nucleus of the resting spermatocyte by the development of the nuclear membrane (Figs. 23, 26, 28, 29 and 30). Throughout the prophases of the first spermatocyte it is still to be seen within the nucleus (Figs. 32, 33 and 43*a*), and after dissolution of the nuclear membrane and formation of the mitotic figure it is cast off to one side of the spindle, where it persists for some time (Figs. 47, 51, 52, 55, 61, 65–67 and 69*b*). With saffranin and malachite green the nucleolus is very evident, coloring bright red, while the chromatin of the resting cell is purple. With iron hæmatoxylin it is not so readily distinguished, but with the Biondi-Ehrlich stain it can be seen as a pink body lying to one side of the spindle.

6. Summary.

The main results of this study may now be briefly summarized as follows:

(1) The spermatogonic chromosomes are joined together in pairs in the synapsis to form sixteen bivalent chromosomes. They may be joined (*a*) in an approximately straight line, (*b*) to form a more or less narrow V, or (*c*) into a more or less complete ring (Figs. 26, 27).

(2) A longitudinal splitting of the chromatin threads takes place at this stage (Figs. 25*a*, *b*, *c*).

(3) The distinctness maintained by the chromosomes up to the formation of the nuclear network of the resting spermatocyte, and the manner of origin of the spermatocytic chromosomes from it, lends support to the theory of their individuality in the resting nucleus (Figs. 28 and 32).

(4) In the structure and mode of origin of the bivalent spermatocytic chromosomes two main types may be distinguished: (*a*) The component chromosomes lie end to end, or (*b*) they lie side by side (Figs. 68*a*, *b*, *c*).

(5) Inasmuch as univalent chromosomes are separated, the first maturation division is reductional (Figs. 48–59).

(6) Sphere substance (idiozome) is not observable, except for a short time during the prophases of the first spermatocyte (Figs. 39 and 43).

(7) The nucleolus of the spermatogonia disappears shortly after dissolution of the nuclear membrane, while that of the spermatocytes, first discovered in the synapsis, persists throughout the divisions (Figs. 8–10, 47, 26, 29, 33, 47, 48, 51, 52, 55, 58, 60*a*, 61, 65–67, 69).

(8) The spermatids become associated in groups to form colonies of nuclei lying in a common plasma (Figs. 73–75).

(9) Within the latter arise bundles of fibres of great length, whose connection with the nuclei, if actual, is very slight and occurs very late, as well as single fibres of greater delicacy which are continuous with the nuclei (Figs. 76–83).

(10) The mature sperm colony consists of a variable number of filamentous nuclei contained, together with the bundle of cytoplasmic fibres, in a tenuous sheath which is flagellate at its anterior extremity (Figs. 84–86).

III. Critical Review of the Literature on Crustacean Spermatogenesis since 1878.

1. Spermatozoa.

a. Review.

Decapoda.

1878. Grobben in his valuable work investigates principally the form of the Decapod spermatozoa and their transformations from the immature to the mature state, as well as the nature of the case (spermatophore) in which they are enclosed. With regard to the spermatozoon of Astacus fluviatilis, he states that the head develops from a structure arising near the nucleus, while the nucleus itself disintegrates. He gives also a review of the literature on Crustacean spermatozoa up to that time, which therefore need not be repeated here.

1883 (1). Herrmann describes the spermatozoa of the Podophthalmia, chiefly the Macrura and Brachyura. The study of the development, he says, shows a series of transitory forms which enable us to seize clearly the bonds of relationship existing between the different adult forms. The transitional forms of some resemble the complete forms of others.

1884. Nussbaum (Astacus fluviatilis) considers the change of the spermatid into the spermatozoon. He traces the gradual condensation and transformation of the nucleus from spermatid to spermatozoon, and the transformation of a large body lying in the cytoplasm into the peculiar "kopfkappe" of the mature spermatozoon (see his Figs. 53–68). He regards the nucleus as the head of the spermatozoon.

1885. Sabatier published a short article on the spermatogenesis of the Decapod Crustacea, principally Astacus.

1886. Gilson describes the spermatozoa of a considerable number of Decapod species, among others Astacus fluviatilis. The structure of the spermatozoon of the latter he delineates more fully than either of his predecessors. The nucleus he shows to be present and saucer-like in shape. It is covered by a layer of protoplasm which is extended laterally into pseudopodic processes. From the centre of the protoplasmic layer sometimes arises a protuberance, to which he gives the name "globule achromatique." The nucleus surmounts a bladder-like vesicle often perforated at the opposite pole. Into this from the centre of the concavity of the nucleus projects what he calls "la tigelle."

1895. Auerbach compares the spermatozoon of Astacus fluviatilis with those of other Crustacea, Insects and Vertebrates, with a view to discovering homologies of head, apex, middle-piece and tail. The cyanophilous, saucer-shaped nucleus corresponds to the head of more highly developed spermatozoa, its pole therefore to the anterior end of a flagellate spermatozoon and the surrounding protoplasm to the sheath of the head. The "globule achromatique" of Gilson is the anlage of the apex. The "tigelle" of Gilson, which Auerbach found to be erythrophilous, he regards as the anlage of the middle-piece. In the genera Pagurus, Eupagurus, Clibanarius and Ethusa the "tigelle" is prolonged into what Auerbach regards as a rudimentary tail. The bladder-like vesicle is perhaps a kind of "Schwanzkappe," possibly comparable with the sheath sometimes surrounding the place of origin of the tail in immature vertebrate spermatozoa. The extremity regarded by Grobben as the head would, according to Auerbach's interpretation, be the tail end. For a more detailed account of the Decapod spermatozoa, of which that of Astacus may be taken as a type, the reader is referred to the works cited above.

Stomatopoda, Schizopoda, Amphipoda.

1885. Gilson, in his excellent and very comprehensive work, describes also the spermatozoa of the Stomatopod Squilla, the Schizopod Mysis and the Amphipod Gammarus. The whip-like spermatozoon of Mysis is strikingly similar in shape to that of the Isopods. That of Gammarus is flagellate and that of Squilla vesicular.

Isopoda.

1883. Herrmann studied among the Isopoda, Ligea, Idotea and Sphæroma. His description is unaccompanied by figures and is difficult to comprehend. The spermatic filaments, he says, are united in numbers varying from eighty to one hundred. The bundles are found lying amongst the cells which line the walls of the tube. He did not find isolated spermatozoa, except in the oviduct of the female, where they retain their habitual form and immobility. The large cell of the vas deferens he considers as homologues of ovarian cells and calls them "ovules males."

1884–1886. Gilson (Oniscus asellus). Groups of six spermatids

("spermatoblaste") were observed surrounding a protoplasmic stem and their origin referred to the small cells in the apical portion of the cæcum. The structure of the nuclei and the changes in them and in the surrounding protoplasm, by which the mass is converted into the mature "spermatophore," are described at some length and illustrated with numerous figures. The name "spermatophore" is applied for the following reasons: "Les cellules spermatozoides sont donc contenus dans un étui resistant derivant de la differentation du protoplasm, c'est-a-dire dans une production particuliere, on pourrait donc appliquer aux faisceaux la denomination de spermatophore." The name "plasmodium pariétal" is applied to the follicle cells and the surrounding protoplasm, and to it is ascribed the function of taking part in the formation of the tails, thus reinforcing the insufficiency of the protoplasm of the germ cells. The tails of the spermatozoa are thus thought to arise in the plasma and to attach themselves to the nuclei "vers le haut." The exact level is not determined. The form of the spermatozoa is compared to that of a whip, the long tail representing the handle and the nucleus the lash. This would seem to indicate that the tail is conceived as being attached to the nucleus at its upper extremity. The entire bundle is said to measure 0.15$\frac{5}{10}$ mm.

The sheath (étui) enclosing the spermatozoa is most evident at the anterior end. The apparent absence of protoplasm around the filamentous nuclei is explained as perhaps due not to degeneration or absorption of the protoplasm, but to a condensation and fusion with the nucleus, perhaps applying itself so closely to the filament that an effect of refraction communicates to it the same coloration This hypothesis is based on results obtained by treating the flagellæ with nuclear solvents. When submitted to the action of potassium carbonate in concentrated solution or strong hydrochloric acid for several days the filaments become scalariform; a skeleton formed of little chambers is seen which communicate with each other, and which were previously filled with the nuclear substance. The characteristic frayed appearance of the bundles is thought to be due to artificial rupture.

The nuclear flagellæ are said to grow considerably after having attained their distinctive form. From the figures given to show this (Figs. 329 and 330, Pl. VIII), it seems probable that this appearance may be due to a portion of the filaments having been broken off by teasing.

The large cells lining the vas deferens are described and also the smaller cells between them. The latter are believed to arise from the larger ones by segmentation. The function of the large cells is said to be the secretion of the fluid which bathes the spermatozoa. The nucleus of these cells is figured as a network of great regularity.

The mature colony of Asellus, as figured by Gilson in Vol. 2 of La Cellule, Pl. X, Figs. 385–395, agrees with that of Oniscus in general appearance. The spermatozoa in the bundle, however, are more numerous and much less compactly bound together. Associated with them in their development is a large cell ("noyau femelle"). The tail is shown to be distinctly continuous with the nucleus. The granular mass surrounding the nucleus at its free end is said to consist of caryoplasm and the remains of the nuclear membrane. Its formation is shown in Figs. 387–393.

A few figures are also given of Idotea.

1886. Wielowieyski, in a short paragraph concerning Asellus, states his opinion that the "noyau femelle" of Gilson is an artificial product, caused by the confluence of the protoplasmic mass with one of the large cells on the margin of the testicle.

Cirrepedia.

1886. Gilson figures the spermatozoa of Lepas anatifera and Balanas perforatus. They are flagellate, the nucleus a slender thread occupying the anterior end.

1894. Ballowitz, K., studied Balanas improvisus Darw. and Lepas anatifera L. He makes the astonishing statement that the head is demonstrable as a distinct structure neither by its form nor by its staining reaction. He mentions the work of Nussbaum (1890) on a Californian Cirrepede (Pollicipes polymerus) in which the head is described.

Copepoda.

1895. Steuer gives a figure to show the spermatozoa of the marine Copepod, Sapphirina gemma. They are flagellate, shaped somewhat like a javelin. He mentions the spermatozoa of the Calanidæ as being of spherical shape.

Ostracoda.

1886. Stuhlmann. The spermatozoa of the Cypridæ are described as having at first the shape of a ribbon, through the length

of which the nucleus runs as a thread. They are stated to increase in size through the assimilation of a secretion of the vas deferens. They then become spirally twisted while in a certain limited section of the vas deferens, presumably by a motion of their own. This is said to be caused by a fibre running spirally the length of the spermatozoon. The mature spermatozoon has the spirally twisted structure of a rope of tow. It contains a twisted central fibre, not visible externally, and the entire structure is surrounded by a hyaline sheath. The spermatozoa are nearly motionless while in the body of the male, but become extremely active in the receptaculum seminis of the female. This is said to be due to the loss of the hyaline sheath. The curious fact is noted that the spermatozoa coming from the right side of the animal are twisted to the left and vice versa.

1889. Müller discovered in the spermatid of Ostracoda one or two "Nebenkerne." These form a "Schwanzstuck" which grows very long and is of complicated structure. Through the middle of the tail runs the central fibre, at or near one end of which the nucleus is located. The spiral twisting is referred to the contraction of the middle one of the three threads which surround the central fibre. He does not agree with the opinion of Stuhlmann concerning the inhibitive function of the sheath while in the body of the male.

Phyllopoda.

1885. Zacharias describes the results of his observations and experiments on the spermatozoa of the Phyllopod, Polyphemus, which he shows to be capable of amœboid movements.

b. Commentary.

The Crustacea as a class show an astonishing variety in the form of the male reproductive elements. Knowledge of their intimate structure is of course at present too incomplete to enable us to discuss at any great length the homologies existing between them. But a rough classification of them according to their external appearance would place the bell-shaped or vesicular form characteristic of the Decapods in one group and the form found in the Isopods, Gammarus, Mysis and Balanus, with more or less elongated nucleus and tail of varying length, in another. The extremely peculiar form of the spermatozoon of the Ostracoda might perhaps be referred to the

latter group. It is possible, and I advance it simply as a tentative hypothesis needing corroboration, that these strikingly dissimilar forms have arisen from a primitive one, simple and amœboid in character like that of Polyphemus.

The ingenious series of homologies drawn by Auerbach between the head, tail, apex and middle-piece of the spermatozoa of Vertebrates and Insects and similar structures in Astacus appears plausible. Since, however, the location of the centrosome and the sphere substance remains undetermined, the homologies cannot be said to be in all respects established. A more detailed and thorough examination of the spermatozoa of the Crustacea, especially of their behavior in fertilization, might extend these homologies. If the spermatozoon of Oniscus be compared with the type most frequently occurring in animals, the part immediately adjacent to the nucleus, the delicate fibril shown in Figs. 77*a*, 79, corresponds in location to the middle-piece. Whether this is in reality the habitation of the centrosome might be discovered through a study of its fate during fertilization. My observations on the spermatogenesis throw no light on the question.

The Isopods are unique among the Crustacea in the formation of colonies of spermatozoa of a nature so close that they appear as units. Concerning their origin in Oniscus, I can confirm M. Gilson's statement that the formation of the bundle takes place in a plasmodium, cell boundaries being for a time entirely absent, and with the main outlines of his account of the changes taking place in the development of the spermatids into the mature colony I am thoroughly in accord.

The number of nuclei entering into a bundle, according to my observations, is not invariably six, but may vary within considerable limits. The number of cytoplasmic fibres is assumed by M. Gilson to be equal to the nuclei, but in his Fig. 328, Pl. VIII, they are shown to be more numerous. As has been already said, I have been unable to convince myself of a direct continuity between these fibres and the nuclei. In his Fig. 320 (an immature spermatophore) the cytoplasmic fibres may be traced directly to the nuclei. I have, however, not been able to obtain images of equal clearness from my preparations. Nor have I obtained anything at all similar to the rings or vacuoles, shown in Gilson's Figs. 328, 329 and 330, near the anterior end of the bundle. In Sphæroma serratum, Gilson states, the continuance of head and tail is very evident, forming an

open and regular ring. The close relationship of nucleus and cytoplasmic fibre in Oniscus is shown only in Fig. 320. In Figs. 323 and 326 they are represented as discontinuous. In Fig. 334 (Asellus) the fibres are pictured as arising independently of the nuclei, although it is shown in later figures that they eventually become attached. If the follicle nuclei and the surrounding protoplasm take part in the formation of the tails, it is only, in my opinion, in so far as they become converted into the substance of the germ cells.

In attempting to reconcile the fact of the direct continuity of head and tail, shown by Gilson so clearly in Asellus and stated by him to be present in Sphæroma, with the lack of demonstrable connection in Oniscus, it occurred to me that the condition in Oniscus might represent a different phase in the evolution of the Isopod spermatozoon. Either the connection, at one time evident, between the nucleus and the unusually long tail may have grown so slight as to be no longer recognizable, or, if the spermatozoon of Oniscus for any reason is to be looked upon as the more primitive form, it may be that the connection, which will later in the course of evolution become more marked, is as yet but little developed. Although in the present state of our knowledge both alternatives may perhaps be considered open, the former seems to me far more plausible, for not only are the land Isopods in other structural peculiarities to be regarded as more specialized than Asellus, but the sperm colony itself in Asellus is less compact and less completely developed as a unit. The obscurity of this point serves to emphasize the desirability of further study of the Crustacean spermatozoa and the establishment of accurate homologies between them.

The "noyau femelle" of Asellus is, in my opinion, to be regarded as homologous with the follicle cells of Oniscus. I am inclined to doubt the correctness of M. Gilson's conclusions as to the origin of the small cells of the vas deferens of Oniscus from the larger ones by segmentation, and, although I have not devoted much time to the elucidation of the point, I think it more probable that the reverse is true, for I have seen the small cells segmenting, but never the large ones.

2. The Earlier Stages in the Development of the Germ Cells in Crustacea, with Especial Reference to the Problem of Reduction.

a. Review.

Decapoda.

1878. Grobben gives almost no figures of the earlier stages and does not consider the subject in detail.

1884. Nussbaum (Astacus fluviatilis) does not distinguish between spermatogonia and spermatocytes. Five figures of mitoses are given in which the chromosomes are shown to be spherical at the beginning of the metaphase, but they soon elongate to a rod-like shape.

1885. Carnoy studied among the Decapods, Astacus fluviatilis, Crangon vulgaris and several species of Brachyura and Anomura. In no case are more than thirteen figures given. It is impossible to determine in every case the generation to which the cells belong. The mode of origin of the chromosomes is not fully traced, and it is impossible to determine with accuracy, therefore, anything with regard to the question of reduction. In the case of Astacus, as far as can be judged from the figures given (Figs. 246*a*, *b*, *c*, *d*, *e* and *f*), the division is transverse. The mitosis figured occurred in August, and, according to vom Rath, it is from this month until December that the final divisions of the spermatogonia and those of the spermatocytes take place. A transverse spermatogonic division is improbable. The chromosomes are shown to arise, however, through the shortening and thickening of rods, resulting from the breaking up of the nuclear network. The transverse division, if it be such, is therefore probably that of the first spermatocyte. The same is perhaps true of Crangon cataphractus (Figs. 247 and 248). Of peculiar interest is the constitution of the chromosomes of Crangon cataphractus, as shown in Figs. 249*a*, *b*, *c*, *d*, Pl. VII. According to these a chromosome in longitudinal view consists of a double row of from three to five granules. A reconstruction of the chromosome from these figures leads to the conception of a rod split longitudinally several times.

Cytoplasmic Structures.—A dense mass, lying within the cytoplasm during the prophases and migrating to the poles of the spindle as it is formed, is shown for Crangon. No centrosome is figured as lying within this mass, to which the name "Nebenkern" is given. The same name is applied to a body lying in the cyto-

plasm in Astacus. This body, however, seems not to be affected by mitosis, but lies passively to one side. In the vicinity of the poles are, however, numerous granules ("corpuscles polaires") (Fig. 246*f*, Pl. VII). The "Nebenkern" of Crangon, according to the description, behaves like the substance designated idiozome by Meves. The "corpuscles polaires" of Astacus may be of a similar nature. For the other forms studied no bodies of any kind lying in the cytoplasm are shown. The substance seems to be unusually prominent in Crangon and Astacus. The cells of both are of large size.

1891. vom Rath settled the question of amitotic division of the germ cells of Astacus in the negative. He states that a minority of the spermatogonia undergo no change at first, but give rise by mitosis to new spermatogonia after the discharge of the ripe spermatozoa. He mentions a case of regeneration of an entire follicle from a single spermatogonium. With the first appearance of the spermatids the follicle cells ("Randkerne") commence to grow in size and divide amitotically. The direct division apparently takes place by a sharp breaking apart of the portions of the nuclei, resembling a slicing. Degeneration of the nuclei follows. At the point of transition between follicle and duct there is often an extraordinary growth of cells by amitosis. The results of his research are interpreted by vom Rath to mean that two kinds of cells have arisen from indifferent epithelium, one dividing mitotically, the other amitotically.

Isopoda.

1884. Gilson states that it is only at certain seasons of the year that the spermatogenesis of these animals can be studied with profit. In the case of Oniscus asellus, from July to November is the most favorable season for obtaining preparation of what he calls the first stage ("premiere etape"). In the case of Asellus aquaticus it is later—about the month of February.

Oniscus asellus.—The cells filling the apical end of the cæca (spermatogonia) are mentioned, and the opinion is expressed that they constitute a reserve mass destined to replace by proliferation the elements organized in the lower part of the tube and later evacuated. Karyokinesis in these cells (spermatogonia) was observed but once, and the stages intervening between them and the spermatocytes were not discovered.

The condition of the lower part of the tube is thus described: "Il y aurait dans les cæcums testiculaires des Oniscus une sort de plasmodium contenant une grande nombre de noyaux et entourant une masse centrale formée d'éléments spermatiques en formation. Ce fait est si étrange qu'on n'ose à peine l'accepter." The amitotic division of nuclei occupying the lower portion of the follicles and referred by Gilson to the germ cells is probably that of follicle cells, for they are described as occupying the periphery of the tube in its median portion.

1885. Carnoy makes the following statement concerning the Isopods (pp. 222, 223): "Chez l'Oniscus asellus, au moment de la plus grande activité cellulaire preludant à la formation des spermatozoïdes, on ne rencontre pour ainsi dire que des noyaux en voie d'étranglement ou de division acinétique. Les figures caryocinétiques y font le plus souvent défaut. Depuis trois ans nous n'en avons rencontré que deux, une couronne equatoriale et une couronne polaire qui sont reproduite dans la Pl. VI, Fig. 227; et cependant nos observations ont été nombreuses et pratiquées à toutes les époques de l'année.

"Nous avons constaté les mêmes phénomènes sur plusieurs animaux du même groupe, sur les Idotea en particulier. La division directe est très fréquente chez ces derniers, et s'y fait normalement. Nous n'y avons point remarque de caryocinêse; mais nous devons ajouter que nos observations sur ces Crustacés bien que fait serieusement ont été beaucoup moins nombreuses que sur Oniscus. Chose remarquable, chez les Idotea la multinuclearité des grandes cellules qui vont se transformer en autant de faisceaux de spermatozoïdes est due exclusivement à la segmentation du noyau primitive. Ces faits sont d'autant plus singuliers que dans un genre voisin, le genre Armadillo, les figures caryocinétiques sont frequents; tandis que les cas de division directe y sont beaucoup plus rares." I have examined testes of Armadillo and also of Porcellio and find that they do not differ greatly from Oniscus as to the manner and frequency of the divisions.

Copepoda.

1890, 1892. The work of Häcker on the eggs of Cyclops has been corrected by the later research of Rückert and need not, therefore, be mentioned here.

1892. Ishikawa gives a figure of the testis of a Copepod cut

longitudinally, showing it to be divided into regions called by him formative, growing and ripening zones. The formative region corresponds in Oniscus to the reserve groups of spermatogonia, the growing region to the apical part of the follicle and the ripening zone to the basal part of the follicle. Ishikawa's conclusions concerning reduction have not been substantiated by recent research.

1894. Rückert. This well-known paper concerns the ovogenesis of the Copepods, *Cyclops strenuus*, *Heterocope* and *Diaptomus*.

In *Cyclops* the number of chromosomes is 22–24. The germinal vesicle shows double threads of chromatin, a longitudinal split having occurred at an early period. At the beginning of maturation these contract to double rods, whose number is the reduced one and which have, moreover, become transversely split. As the spindle is formed the chromosomes come to lie in the equator, with the longitudinal split at right angles to the axis of the spindle. The first division is thus equational. In the second division the chromosomes are separated along the transverse split, and this division is therefore reducing.

In *Heterocope* and *Diaptomus* open rings are formed which, through condensation, become the tetrads. The plane of the first division is not so easily determined for these Copepods. In the opinion of Rückert the first maturation division of Diaptomus is equational.

1895. Häcker studied the ovogenesis of the Copepod, *Canthocamptus*. The reduced number of chromosomes is twelve. There are apparently two divisions of the ovogonia. The last division is followed (1) by a transverse breaking apart of a doubly split thread and a shortening and thickening of the segments so that twelve double rods are produced. Some of these are transversely split. Or (2) the last division of the ovogonia is followed by a condensation and longitudinal division of the thread as a whole and a subsequent breaking apart of the thread into twelve double rods. These become transversely split and form chromosomes corresponding to the tetrads of the first mode. In either mode the changes follow immediately upon the last division of the ovogonium, and no true reticulum is formed in the germinal vesicle. Since the width of the chromosomes is equal to their length, it is impossible to settle the question as to the order in which the longitudinal and transverse divisions occur.

1895. vom Rath describes the ovogenesis of marine Copepods

mentioned by him in his earlier works on *Gryllotalpa* and *Salamandra*. He studied the genera *Euchæta*, *Eucalanus*, *Anomalocera* and *Pleuromma*. He calls attention to the differences that may exist between the ovogenesis of different species of marine Copepods and between the ovogenesis and the spermatogenesis of the same species. His conclusions on the subject of reduction agree substantially with those of Rückert. Particularly in the case of *Euchæta marina* and *Eucalanus attenuatus* is the aspect of the first maturation figure similar to that of Cyclops. Here, too, the division seems to be equational.

Ostracoda.

1898. Woltereck describes a well-marked synapsis zone in the ovary of a parthenogenetic Cyprid. He rejects, as not applying to the object which he studied, the theories of Moore, Brauer and Häcker concerning the relation of the synapsis to the last ovogonic division and to the processes of reduction and maturation. "Von 'Reduktion,'" he says, "ist nicht die geringste Andeutung vorhanden, von der Reifungstheilung sind die Eier noch durch eine lange Phase getrennt, in der das Chromatin kaum sichtbar ist and gegen die Auffassung als Dispirem die excentrisch Zusammenballe bei deutlich vorhandenem Nucleolus, sowie das Vorhandensein aller Uebergänge aus einem lockeren, hellen Fadenknauel in die Synapsis und aus ihr in die segmentirten Chromosome."

Phyllopoda.

1892. Brauer thus summarizes his results on the ovogenesis of Branchipus: "Die Beobachtungen, welche ich bei Branchipus gewonnen habe, zeigen nun folgendes Bild:

"1. Keimbläschen: durch Quertheilung entstehen 6 Schleifen; eine neue Quertheilung erhöht ihre Zahl auf 12. Dann folgt eine doppelte Langspaltung. Resultat: 12 viertheilige Chromosomen bil den die Aquatorialplatte der ersten Richtungsspindle" (p. 53). In describing the Figs. 8 and 9, Taf. I, upon which he bases this conclusion, he says: "Ich will gern zugeben, dass diese Beobachtung schwierig sind und eine Taüschung möglich ist, doch muss ich vorheben, dass ich kein Bild gesehen haben, welches eine Vermehrung der 12 Faden durch eine Quertheilung auf 24 zweitheilige auch nur andeutete und spatere Verklebung von je zweitheilige zeigte. Solche Bilder, welche ganz ähnlich aussehen

müssten wie das in Fig. 1 dargestellte, waren mir, glaube ich, nich entgangen."

1893. Brauer. The study of the closely related Phyllopod Artemia was undertaken by the same author with the object of ascertaining whether reduction took place in parthenogenetically developing eggs.

The number of chromosomes in the germinal vesicle is eighty-four, and their structure is quadripartite, *i. e.*, each consists of four spheres. In the first maturation division two of these spheres are separated from the others. After this has taken place the maturation may proceed in two different ways. The second polar body may be formed and the elements of the dyad separated, or there may be an abortive attempt to form the second polar body, the chromatin, however, remaining undivided and the elements of the dyad not separated.

Cleavage and further development of the egg may take place in both of the above cases. In the first case it is necessary for this that the second polar body be drawn back into the egg, where it acts as would a male pronucleus. In the second case the nucleus left within the egg after the formation of the first polar body, becomes the cleavage nucleus. In the first case the somatic number of chromosomes is 168, in the second case 84.

It thus appears that the tetrads of the germinal vesicle are bivalent chromosomes and that the actual reduction may or may not take place.

1893. Moore published the results of his studies on the reproductive elements in Apus and Branchipus. With regard to Branchipus, the chief stress of the paper is laid upon the relation between karyokinesis and protoplasmic structure, the author believing "that the divisional phenomena of these cells are intimately related to a protoplasmic structure, which might be fitly described as 'Schaumplasma,' and one of the initial physical impulses toward metamorphosis is a fusion of some of the intra-nuclear globules; and a considerable portion of the complicated karyokinetic figures, with their centrosomes, pseudosomes and dictyosomes, appear to be the logical as well as the actual consequence of the continuance of this process."

The question of reduction is not entered upon in much detail. From the nucleus of the resting spermatocyte, however, are shown to arise ten chromosomes of dumbbell-shape. These become

arranged in the equatorial plate with the transverse constriction in the plane of the equator. This division consequently is apparently reducing. No longitudinal split is shown and the second spermatocytic division is very inadequately worked out.

b. Commentary.

Although agreeing with many points in the description of Gilson concerning the metamorphosis of the spermatids of Oniscus, my observations do not entirely coincide with his account of the earlier stages. The statement defining the most favorable season for obtaining preparations of the first stage does not hold true for the locality of Philadelphia, for I have sectioned material collected during every month of the year, except December and January, and have not found one month to be preferred over another with regard to the abundance of any particular stage.

I feel sure that the function of replacing the evacuated elements which he ascribes to the spermatogonia is the true one, but that their multiplication takes place by direct division I am unable to believe. On the one hand the weight of the evidence of modern research is against the occurrence normally of amitotic division in the germ cells. Moreover the work of vom Rath on Astacus creates a strong probability that the phenomena are similar in Oniscus. I have never seen amitotic division in the germ cells of Oniscus, and believe that the error arose from a failure to distinguish between the germ cells and the follicle cells. I cannot help a feeling of surprise that mitosis should have been so infrequently seen both by M. Gilson and his colleague, M. Carnoy. It is true that the mitoses of the spermatogonia are scattered, and occasionally no spindles at all will be met with in a follicle, but by cutting a sufficient number of sections cell division will be abundantly seen.

With regard to the question of reduction in the Crustacea, my results, much to my own surprise, do not coincide with those obtained by Rückert and vom Rath in the Copepods. The case in Cyclops is so clear that it seems to admit of no doubt, and its very clearness makes it probable that the divisions take place in a similar manner in a form so closely allied as Canthocamptus. The figures given by Häcker of this object do not, however, conclusively prove this to be the case, since the tetrads are cubical in shape, the length no greater

than the width. Indeed Häcker himself says of this object that it is not adapted to the solution of the problem of reduction. The like may be said of Artemia.

With Brauer's results on Branchipus, those obtained with Oniscus likewise do not agree. The double longitudinal split claimed by Brauer for the chromosomes of Branchipus is not shown in the figures with the clearness that might be desired. An oblique view of an elongated chromosome in Fig. 8 shows it to be split longitudinally, not twice but only once. In the absence of direct evidence to the contrary, the Figs. 8 and 9 might be explained equally well on the assumption that the twelve tetrads represent two univalent chromosomes longitudinally split and joined end to end.

In Oniscus, inasmuch as the first division separates two originally distinct chromosomes and the second presumably divides the chromatin longitudinally, the manner of reduction resembles that of Insecta as described by Henking (1890–'92), Paulmier (1899) and Montgomery (1898, '99).

If my interpretation of the method of reduction in Oniscus be correct, and that of Rückert concerning reduction in Cyclops be equally so, it becomes clear that the cell generation in which the true reduction takes place need not be the same for all members of a given class of animals. The order in which the reduction and equation divisions take place is, therefore, relatively unimportant; the significant thing, so far as our knowledge at the present day goes, appears to be that in the Arthropods both divisions should take place. Further research alone can show whether the apparent cases of transverse division in the first spermatocytes of Astacus, Crangon and Branchipus are really such. To the future must also be left the question as to which method of reduction, the Copepod or the Isopod type, is the rule among Crustacea.

M. Louise Nichols.

January 10, 1901.

Explanation of the Plates.

All of the figures, with the exception of 1, 2 and 68, are camera drawings made at the level of the microscope stage, and all except 3, 4*a*, 5, 6, 84–86, were drawn with a Zeiss homogeneous immersion objective $\frac{1}{12}$, ocular No. 6, tube length 100 mm. In those marked * the chromosomes are not all shown.

Plate XI

1. Free-hand drawing to illustrate the male reproductive organs of one side. *a*, *b*, *c*, lobes of the testis; *v*, vas deferens; *p*, penis; *x*, suspending tissue.
2. Lobes of the testis in longitudinal section (semi-diagrammatic). *a*, *b*, *c*, as before; *spg.*, spermatogonia; *f. c.*, follicle cell.

Plate XII

3. Longitudinal section of the vas deferens (Zeiss ocular 4, obj. AA). *b*, *c*, lobes of the testis.

4*a*. Small portion of the wall of the anterior region of the vas (oc. 6 obj. D).

4*b*. Secretory cell from the anterior region of the vas.

Plate XIII

5. Small portion of a testis lobe in longitudinal section. *f. c.*, follicle cells; *m. l.*, muscular layer (oc. 6, obj. D).
6. Cells from the suspending tissue (*cf.* Fig. 1, x) (oc. 6, obj. D).
7. (*a*) Spermatogonium in an early spireme stage; *ncl*, nucleolus. Centrosomes beginning to divide. (*b*) Resting spermatogonium with large masses of chromatin, probably beginning to degenerate.

*8, *9, 10. Later spireme stages.

11. (*a* and *c*) Resting spermatogonia. (*b*) Spireme beginning to segment.
12. Equatorial plate in side view.
13. (*a*) Equatorial plate in pole view. (**b*) Spermatocytic prophase. *m. l.*, muscle layer.
14. Equatorial plate in side view, showing the longitudinal split in the chromosomes.

*15. Metaphase.

16. Approximate pole view of a stage similar to 15.
17. Anaphase.
18. Late anaphase. Mid-body.

*19, *20. Reconstruction of the daughter nuclei. In 20 the mid body has migrated to the periphery.

*21. (*a* and *b*) Reconstruction of the daughter nuclei. (*c*) Degenerating spermatogonium.

Plate XIV

22, 23–28. Synapsis. 26. 1–16, chromosomes.

27. Different forms of the chromosomes in the synapsis.
29. Formation of the nuclear membrane.
30. Resting spermatocyte. *spg.*, spermatogonium.
31. Irregular arrangement of the nuclear network, occasionally seen just before the formation of the nuclear membrane.

PLATE XV

32, *33–47. Prophases of the first spermatocyte. 44. 1–16, chromosomes.

46 and 47. Strongly decolorized sections showing the longitudinal split of the chromosomes. Divergence of the centrosomes.

48. (*a*) Side view of the equatorial plate of the first spermatocyte. (*b*) Anaphase of the first spermatocyte.

49–53. Equatorial plate of the first spermatocyte in side view.

54. Chromosomes of the first spermatocyte, showing the longitudinal split.

55, 56. Pole views of the equatorial plate of the first spermatocyte.

57. Slightly oblique view of the same.

PLATE XVI

58. Anaphase (side view).

59. Anaphase (pole view).

60. Anaphase (tangential sections).

61. Telophases.

62. Side view of the equatorial plate of the second spermatocyte.

63. The same more strongly decolorized.

64. Pole view of the same.

65. Metaphase.

66, 67. Telophases.

68. (*a* and *b*) Mode of formation of the two main types of chromosome in the first spermatocyte. (*c*) Intermediate form.

69, 70. Reconstruction of the nucleus of the spermatid.

70. Disappearance of the cell boundaries. *x*, remains of degenerated cells.

71. Variation in the appearance of the spermatid nucleus.

72. Commencing elongation of the spermatid nucleus.

73. Group of spermatids from near the margin of the testis lobe. Appearance of cytoplasmic striations (hæmatoxylin and Bordeaux red).

PLATE XVII

74–79. Further development of the spermatids.

74. Stage succeeding 72. (*a*) Longitudinal; (*b*) transverse section (iron hæmatoxylin).

75. Longitudinal section (iron hæmatoxylin).

76. Longitudinal section (Biondi-Ehrlich). The middle figure alone is complete anteriorly.

77. (*a*) Longitudinal; (*b*) oblique section (iron hæmatoxylin).

78, 79. Nearly mature sperm colonies in incomplete longitudinal section (hæmatoxylin and Bordeaux red).

80. Cross sections at different levels of nearly mature sperm colonies. (*a*) anterior to the nuclear region; (*b*, *c* and *d*) nuclear region; (*e*), posterior to nuclear region (saffranin and malachite green, black = red, gray = green).

PLATE XVIII

81. Cross sections of colonies of about the same stage (iron hæmatoxylin).
82. Cross sections of colonies at a later stage (iron hæmatoxylin).
83. Group of spermatids with convoluted nuclei. Cytoplasm of the individual cell still evident (iron hæmatoxylin).
84. Mature sperm colony (Delafield's hæmatoxylin) (oc. 6, obj. D).
85. The same (hæmatoxylin and Bordeaux red).
86. The same (oc. 4, obj. AA).

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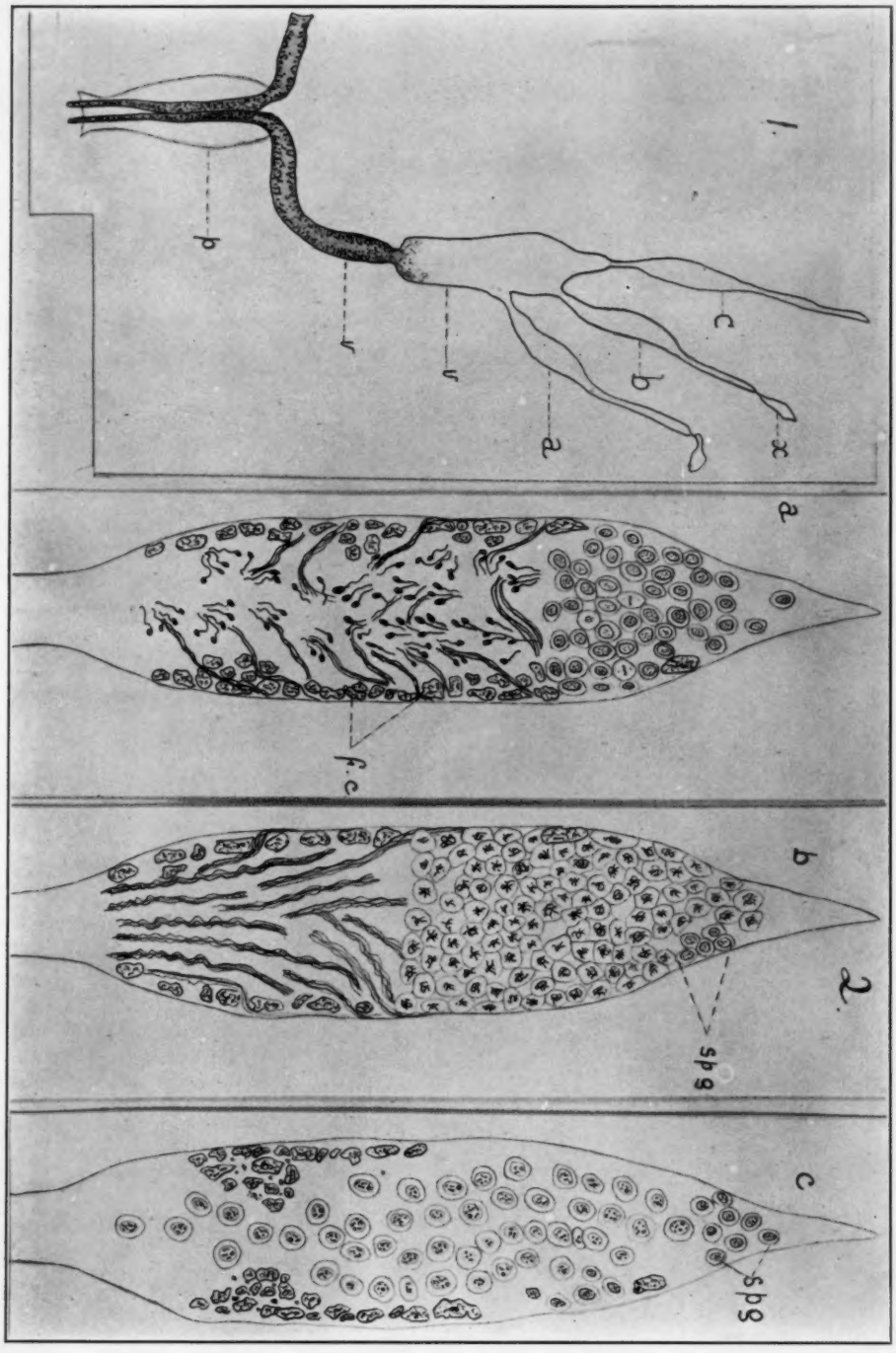

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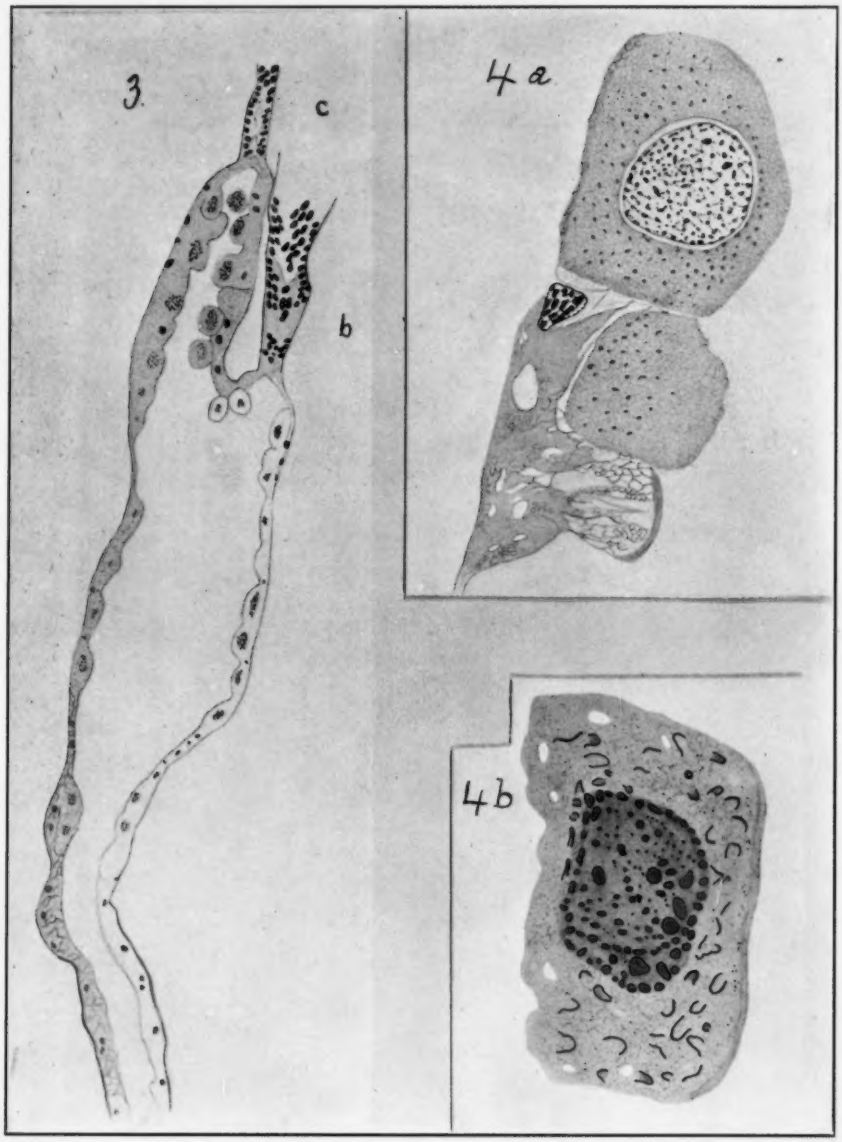

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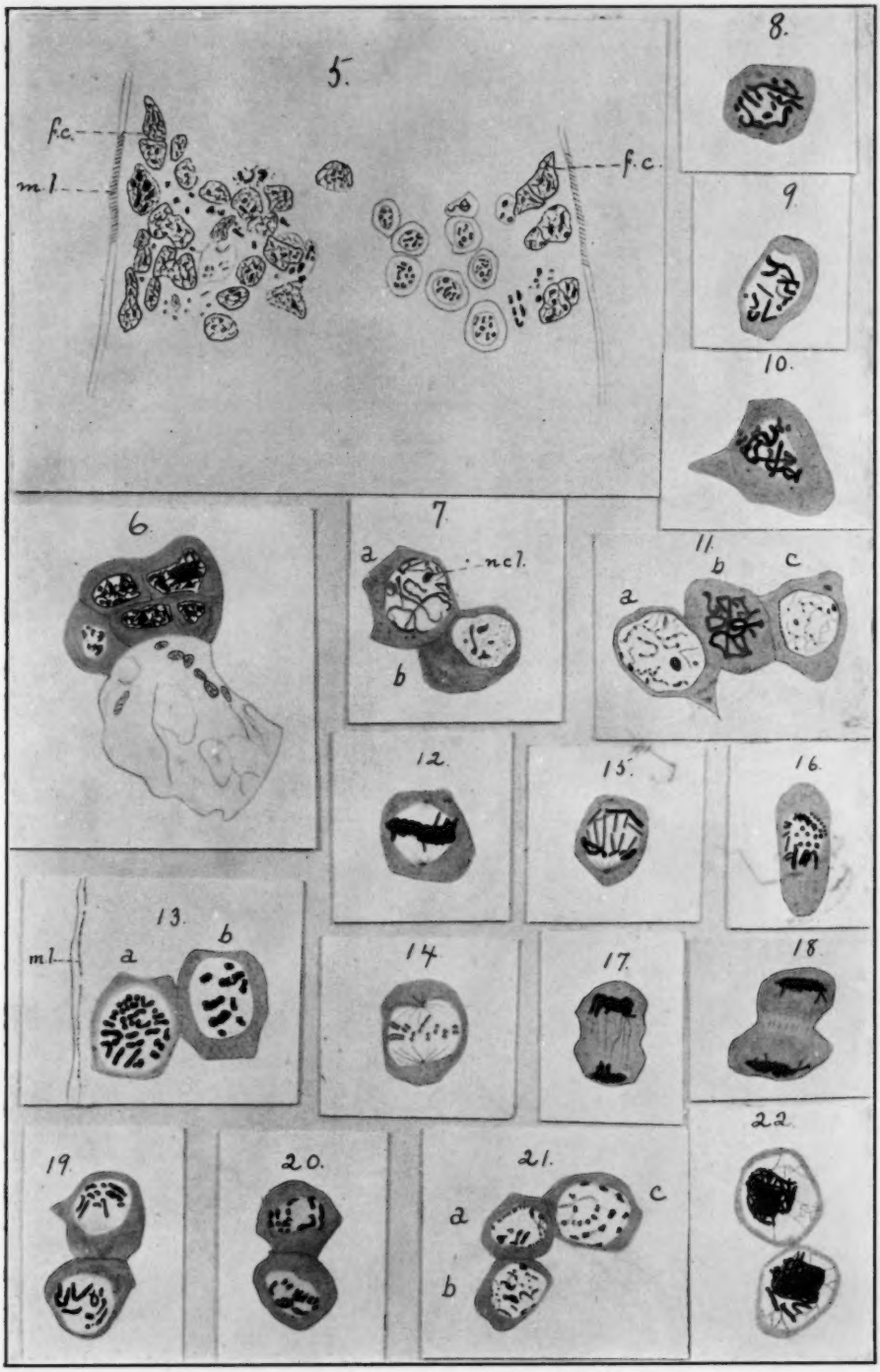

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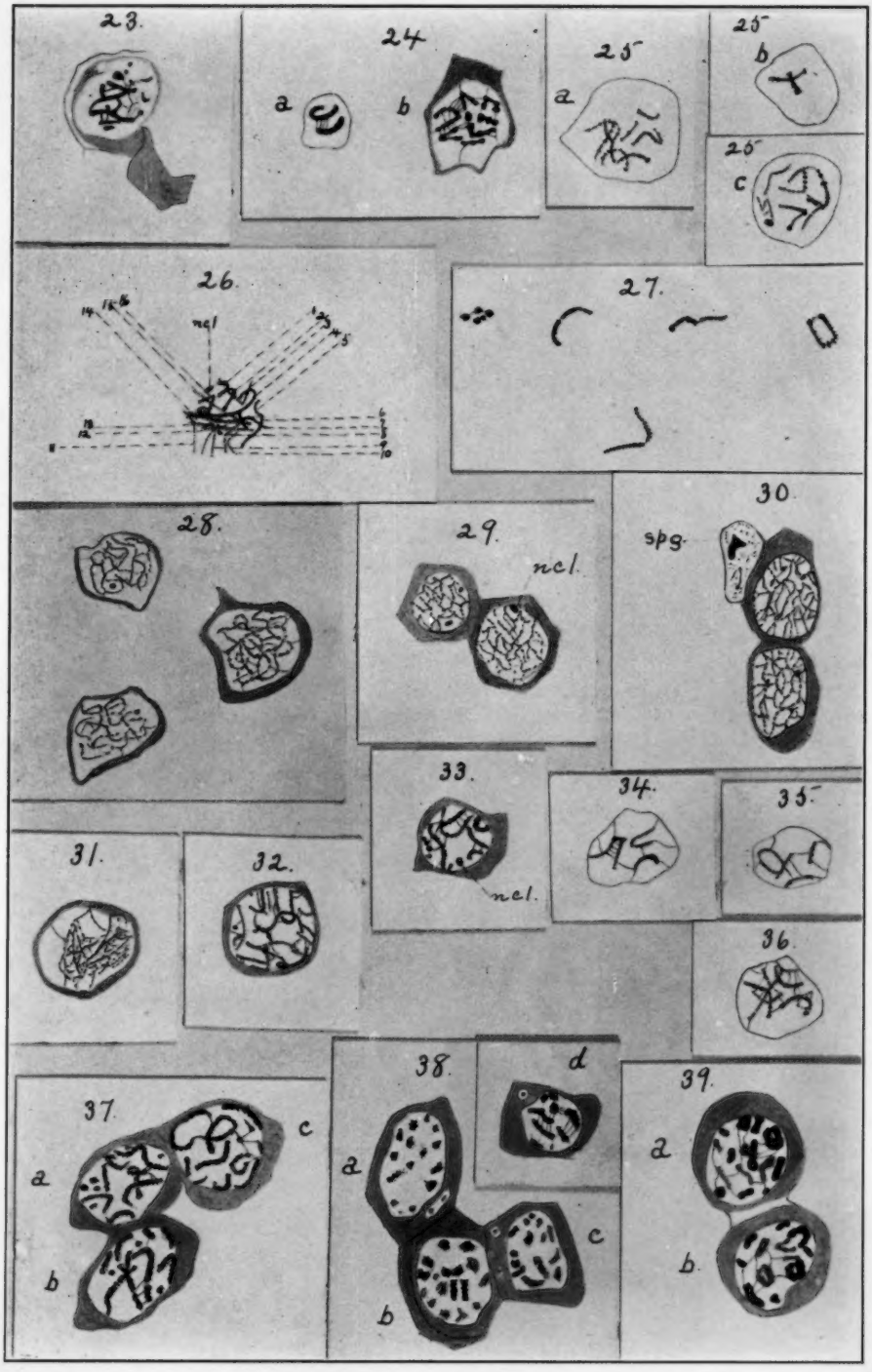

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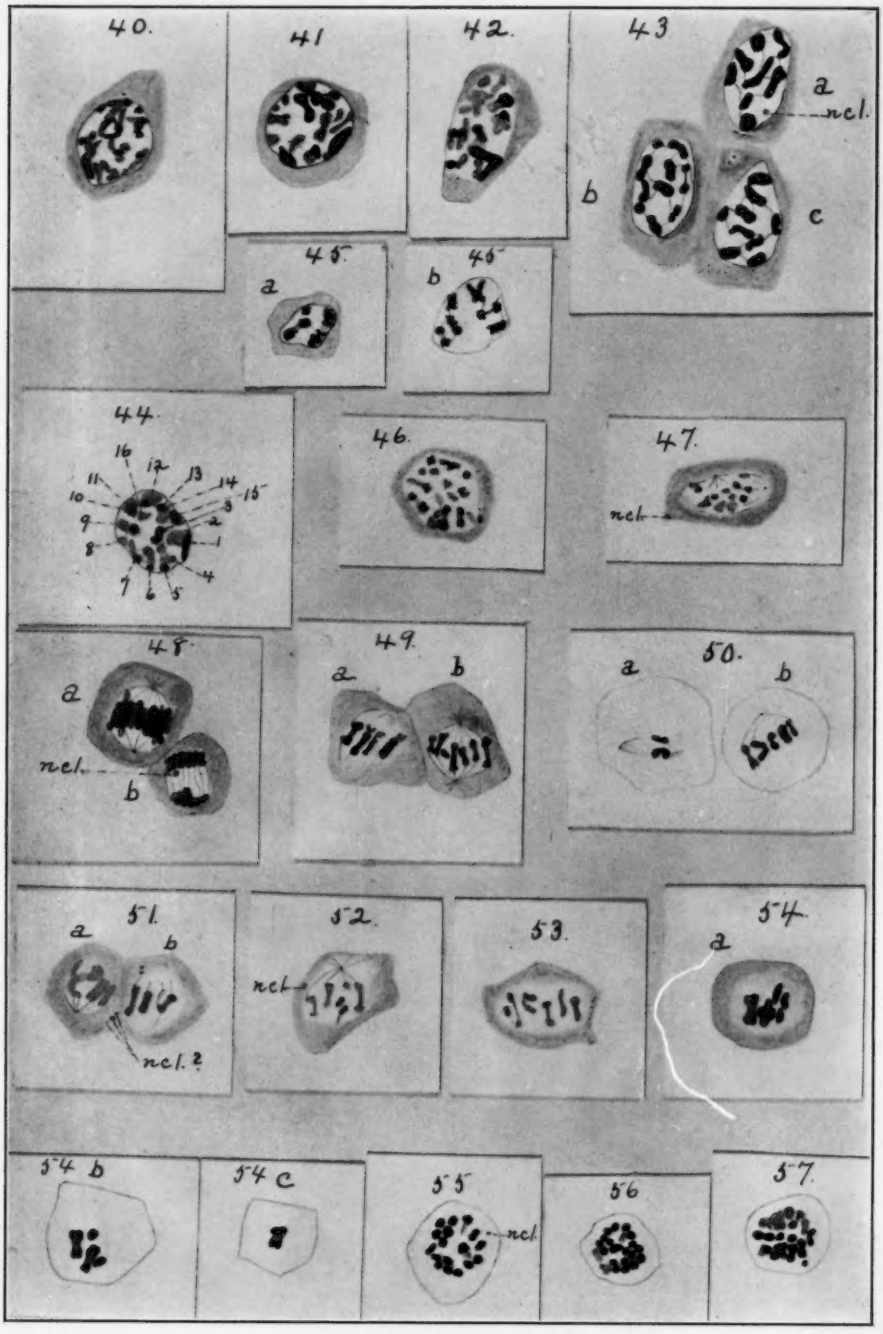

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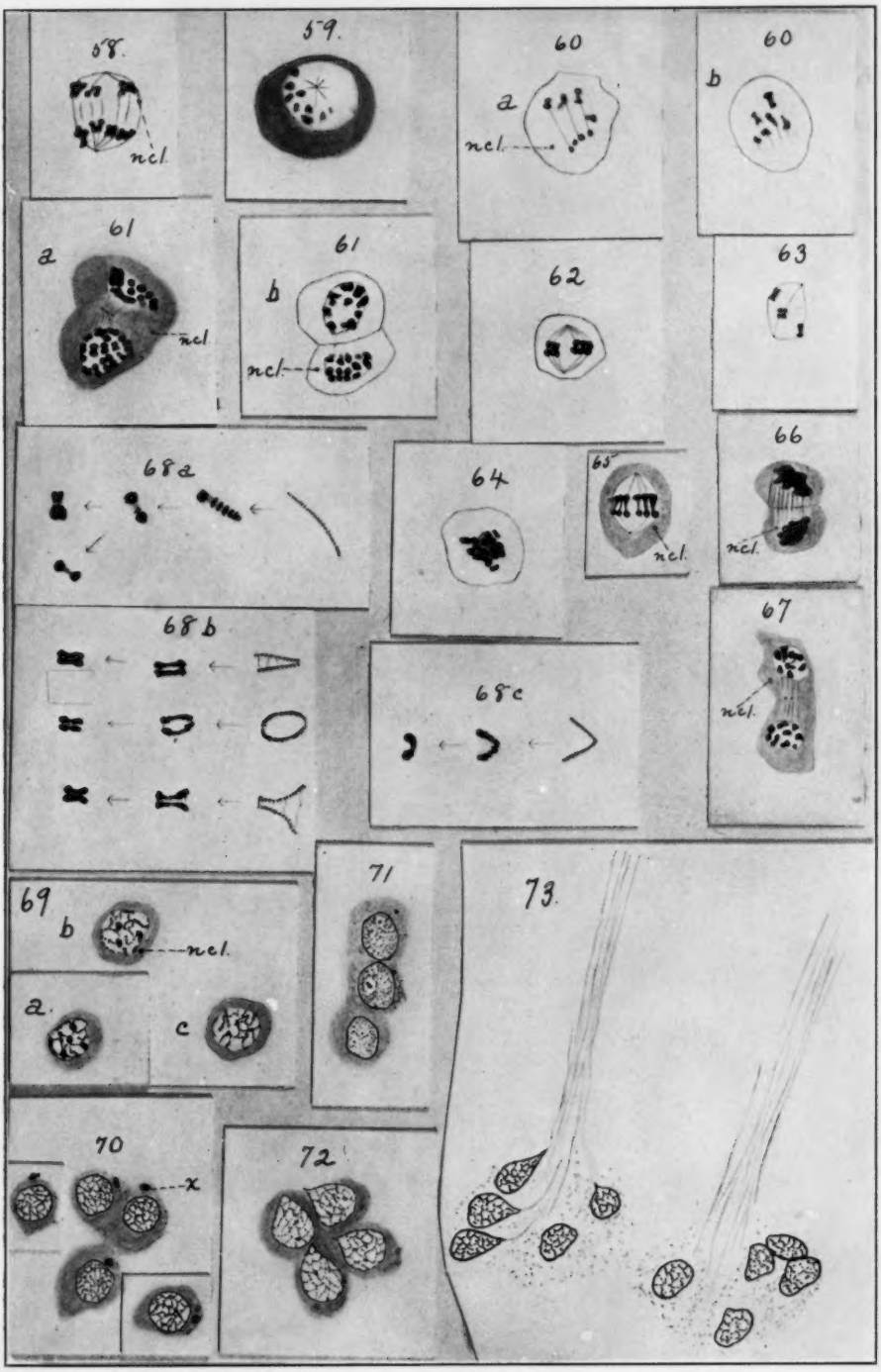

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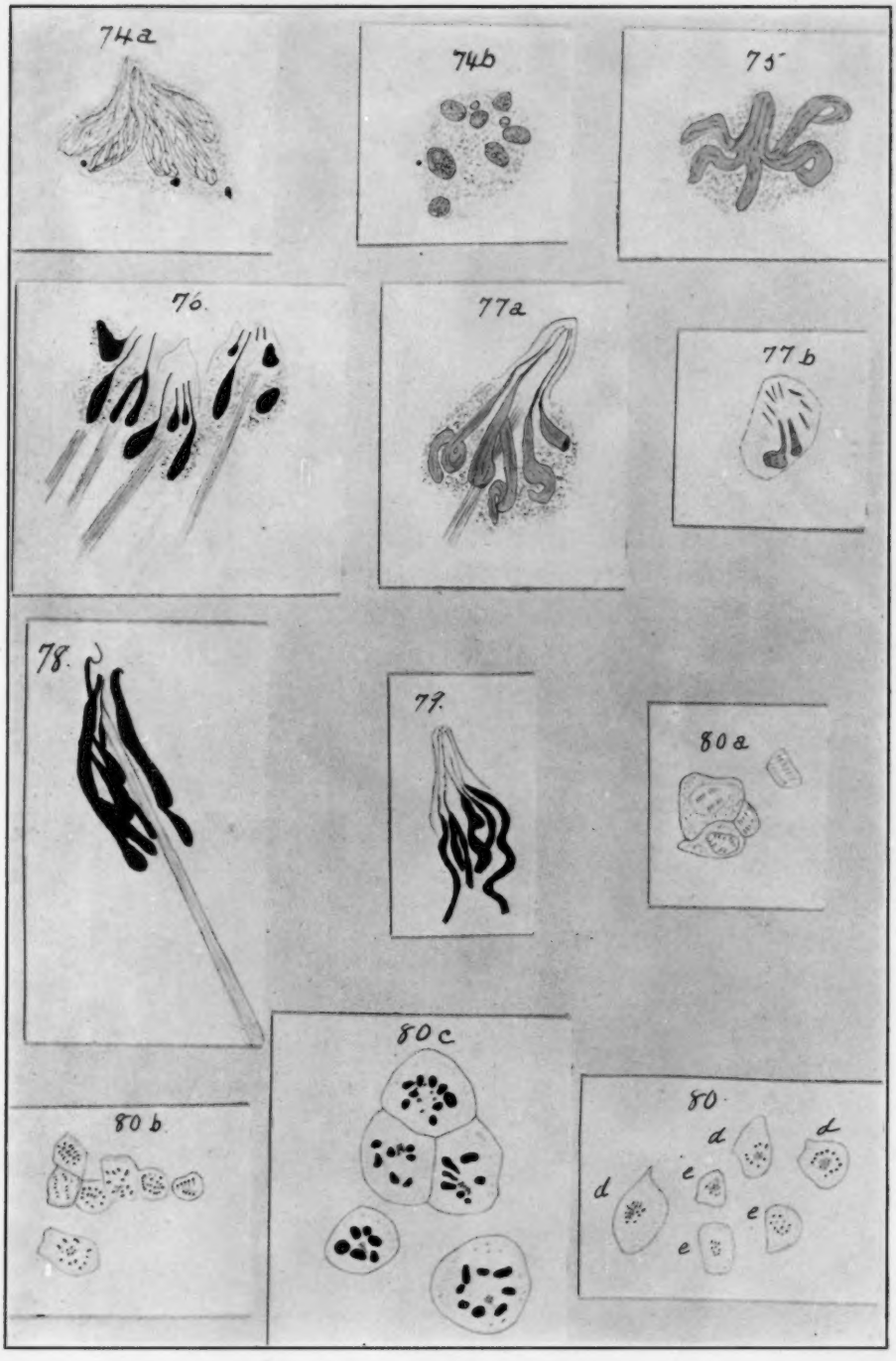

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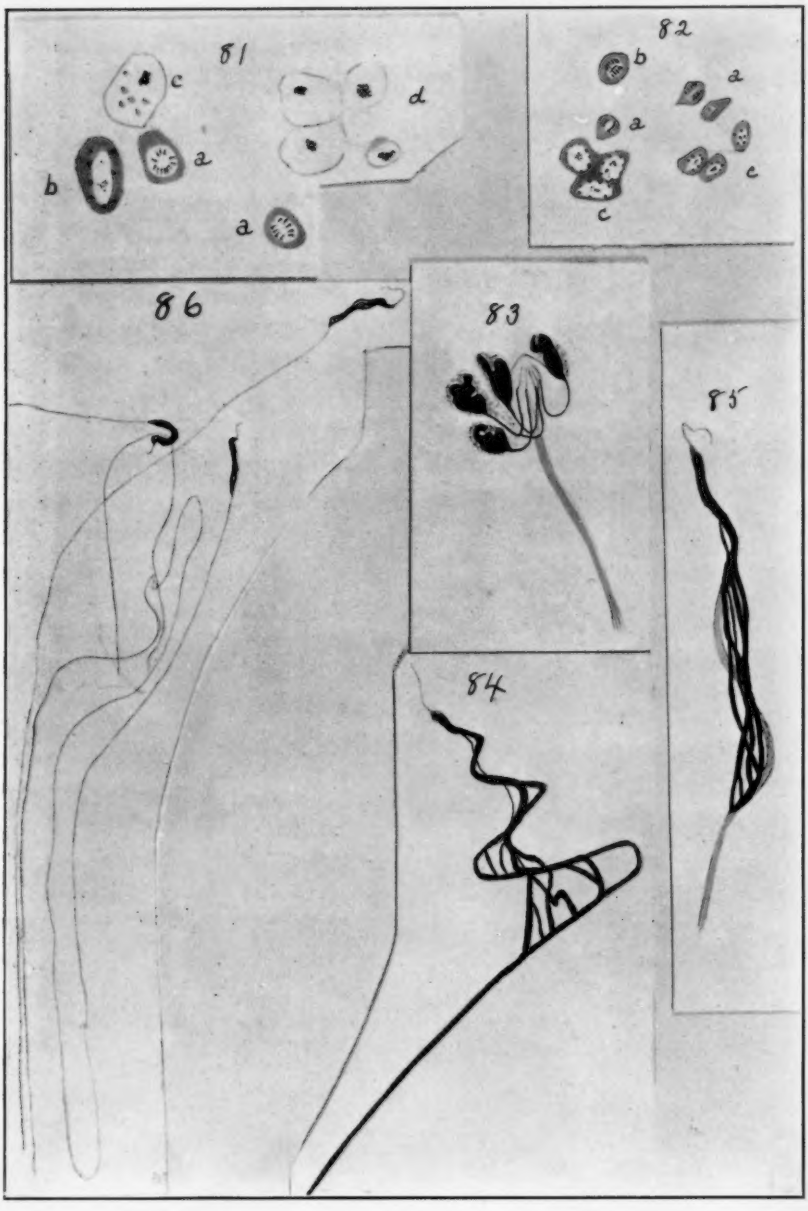

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